DIVERSITY, ABUNDANCE AND FATE OF ICE ALGAE AND PHYTOPLANKTON IN THE BERING SEA

By

Anna Szymanski

RECOMMENDED:

Dr. R. Eric Collins

Dr. Katrin Iken

Dr. Rolf Gradinger, Advisory Committee Chair

Dr. Katrin Iken
Program Head, Marine Science and Limnology

APPROVED:

Dr. Mike Castellini
Dean, School of Fisheries and Ocean Sciences

Dr. John Eichelberger
Dean of the Graduate School

12/8/14
Date

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A

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Anna Szymanski, B.A.

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Abstract

Sea ice algae are an essential part of Arctic and subarctic ecosystems. They significantly contribute to total algal primary production, serve as an early spring food source for both pelagic and benthic biota, and can seed the spring phytoplankton bloom during periods of ice melt. In the subarctic Bering Sea, virtually nothing has been known about the composition of the ice algal community, its magnitude, and its connection to pelagic and benthic ecosystems. This study, therefore, focused on the diversity, abundance, and ultimate fate of ice algae in the Bering Sea using sea ice, water and sub-ice sediment trap samples collected during two spring periods: ice growth (March to mid-April) and ice melt (mid-April to May) in 2008 and 2009. Ice algal species composition was comparable to those in Arctic regions. The phytoplankton species inventory was similar to that found in the overlying ice, suggesting that the spring phytoplankton were seeded from the ice algae. Algal abundance in the ice was on average three orders of magnitude higher than in the water column throughout both periods, as the extensive Bering Sea ice cover in 2008-2009 delayed the phytoplankton bloom. There was a substantial increase in the vertical flux of algal cells beneath the ice during the period of ice melt, but measurable amounts appeared as early as mid-March. The majority of this flux was composed of healthy algal cells, making it a rich food source for benthic organisms. Differences in the relative species composition between ice and trap samples indicate that algal fate was influenced by the species specific sinking rate of algal cells, among other factors, in the water column. In conclusion, ice algae in the Bering Sea are diverse and abundant, and contribute to both pelagic and benthic systems.

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Introduction

Seasonal sea ice is among the most defining features of the subarctic Bering Sea shelf, influencing both the physical and biological structure of the water column not only during periods of ice cover but throughout the year (Hunt et al. 2008; Stabeno et al. 2010; Stabeno et al. 2012a). Ice extent and the timing of ice melt dictate the development of primary production in the water column, and the ice itself supports a rich growth of ice algae long before the first spring phytoplankton bloom. Despite the generally acknowledged importance of ice algae as a food source for sympagic, pelagic and benthic organisms in the Arctic (Bluhm and Gradinger 2008), virtually nothing is known about the diversity of the Bering Sea ice algal community, its connection with the underlying phytoplankton, and its ultimate fate during the annual ice melt in the spring.

Sea ice can cover the entire Bering Sea shelf during winter and spring, extending over an average of 200,000 km^2 before completely retreating each summer (Wendler et al. 2013). The ice impacts the climate, oceanography and productivity of the Bering Sea, mediating the exchange of heat and gases between the atmosphere and the water, influencing light availability, water temperature and salinity, and providing a physical habitat that is essential for many marine mammals. The ice also supports a large community of microorganisms within it, which has been virtually unstudied. In the Bering Sea, Alexander and Chapman (1981) found high chlorophyll concentrations within the ice, indicating a substantial standing stock of ice algae, but little additional knowledge on the structure and importance of this community has been gathered in the past three decades.

The contribution of ice algae to the overall primary production in the Bering Sea is thought to be up to 10% of the annual total (McRoy and Goering 1974; R. Gradinger unpublished data). While this fraction is less than stated for other Arctic regions, where the proportion can be over half (e.g., Gosselin and Levasseur 1997), the timing of the ice algal bloom makes it an essential part of the Bering Sea ecosystem. Across the Arctic, ice algal blooms can precede phytoplankton blooms by as much as three months (Leu et al. 2011). This makes ice algae a crucial first food source for zooplankton during the early spring (Tourangeau

and Runge 1991; Michel and Legendre 1996; Durbin and Casas 2014). Ice algae can also contribute a significant proportion to the total carbon export to the benthos, providing a high quality food source for benthic organisms (e.g., Boetius et al. 2013). In some seasonally ice-covered seas, ice algae can remain viable in the water column after ice melt, seeding the spring phytoplankton blooms and further extending their importance in the ecosystem (e.g., Michel et al. 1993; Haecky et al. 1998). Ecosystem modeling studies have highlighted the relevance of seeding for the development of the spring phytoplankton bloom in the Bering Sea (Jin et al. 2007), but direct evidence based on field observations has been lacking. While a unique, short-lived phytoplankton community occurs in association with the receding ice edge, the origin (ice versus plankton) has remained unknown due to the lack of information on the algal community composition within the ice (Schandelmeier and Alexander 1981). Similarly, the partitioning of the often high vertical flux of organic matter beneath the ice in the Bering Sea between phytoplankton and released ice algae has not been determined (Cooper et al. 2013).

Based on the above outlined substantial gaps in our understanding of early spring sea ice algal and phytoplankton bloom characteristics in the Bering Sea, I defined three major objectives for this study: first, to characterize the diversity and abundance of the Bering Sea ice algal community during periods of ice growth and ice melt; second, to determine the influence of ice algae on the phytoplankton community during these periods; and third, assess the possible fates of ice algae during ice melt through the examination of ice, water and sub-ice sediment trap samples. I predicted that the ice algal abundance would exceed that of the phytoplankton until the start of the ice-edge bloom, which I expected to coincide with a significant increase in vertical flux rates; I further hypothesized that ice algae would contribute to seeding the ice-edge phytoplankton bloom during the spring.

Materials and methods

Sample collection

The Bering Sea is dominated by a broad shallow shelf that extends over 1000 km south of the Bering Strait with an average depth of only 65 m (Wang et al. 2007). Ice algae and phytoplankton were collected from across the shelf as part of the Bering Sea Ecosystem Study during three spring cruises on the USCGC Healy: HLY0802 April 4-30, 2008; HLY0901 March 17-27, 2009; and HLY0902 April 7-May 2, 2009. Sampling occurred under a range of ice conditions. I defined two ice periods based on observed changes in the temperature gradient between the surface and bottom of the sea ice (R. Gradinger, unpublished data): the ice growth period was defined as prior to day 100 of the year, while the ice melt period was defined as extending from day 100 of the year until the end of sampling. This approach eliminated effects of regional and inter-annual differences in the physical growth regime of the sea ice algae. Ten stations were sampled during each period for a total of 20 stations, extending across the central Bering Sea shelf south of St. Lawrence Island (Fig. 1; 58.21-63.48ºN; 167.75-178.90ºW).

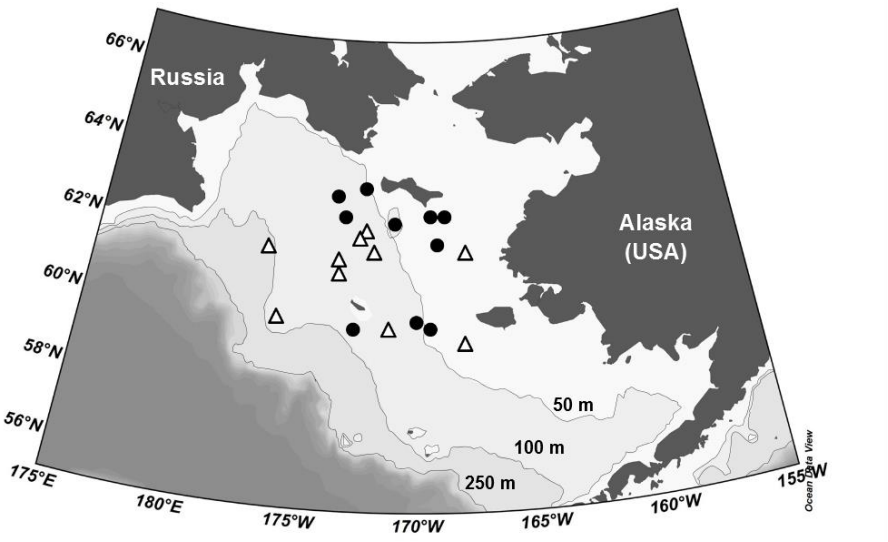

Figure 1. Bering Sea station map during spring 2008-2009. Black circles indicate stations sampled during the period of ice growth (before day 100 of the year), open triangles indicate stations sampled during the period of ice melt (day 100 and later of the year).

From each station, a set of three algal samples was collected from the ice, water and sub-ice sediment traps. Ice cores were obtained using a Kovacs ice corer (diameter 9 cm). The bottom 2 cm of the ice core were used for the analysis of the algal community; this segment was melted slowly in filtered sea water to prevent osmotic stress to the ice algae (Garrison and Buck 1986). Phytoplankton was collected at 5 m water depth through a core hole in the ice using a Kemmerer water sampler. To determine the vertical flux rate of algal cells, cylindrical sediment traps (KC Denmark; diameter 10 cm, 1:10 aspect ratio) filled with filtered seawater were deployed beneath the ice at a depth of 5 m for 4-6 hours. Algal samples were fixed in a 1% final concentration of buffered formaldehyde-sea water solution. Samples from HLY0902 were lost; however, a second set of ice and sediment trap samples were taken on this cruise for a separate study. These samples were collected as described above; however, melted ice and sediment trap samples were then concentrated over a 20 μm filter prior to fixing. Large cells (> 20 μm) contributed over 94% to the algal abundance in the ice and traps in the unfiltered samples from 2008, and there were no significant differences when I compared ice algal abundance (cells l^{-1}) and vertical flux rate (cells m^{-2} day^{-1}; t-tests, $p>0.05$ for both comparisons), and the relative species composition in ice and trap samples (PERMAOVA, $p>0.05$ for both comparisons) between the filtered samples from 2009 and non-filtered samples from the same time period in 2008. Therefore, I included these samples in the analysis; however, there were no water samples available from HLY0902.

A set of environmental variables were recorded at each station. A CTD (SEACAT 19plus) was lowered by hand through auger holes in the ice to measure under-ice hydrography. Temperature, salinity and light intensity in the PAR range (400-700 nm) were recorded in 1 m increments from the surface to approximately 20 m depth. For comparison among stations and relation to ice data, I used the light data at 2 m depth to minimize errors due to the corer hole (Petrich et al. 2012). For inorganic nutrient analysis (i.e., nitrate, phosphate, silicate) water samples were collected from the ship using Niskin bottles every 10 m starting at the surface. Ice thickness was recorded from the length of ice cores, and snow depth was averaged from 10 random measurements at each station. Approximate percent ice cover and primary ice type (e.g.,

first year ice, young grey-white ice, young grey ice, pancake ice, new ice, brash ice; Eicken et al. 2009) were recorded by shipboard observers; primary ice type was assigned a numerical value according to Eicken et al. (2009). Day length at each station was calculated using the U.S. Naval Observatory website (http://aa.usno.navy.mil/data/docs/rs_OneDay.php). Environmental data used in this study are available online at http://beringsea.eol.ucar.edu/.

Analysis of algae

I processed all algal samples at the University of Alaska Fairbanks in 2013-2014. After bringing algal cells into homogenous suspension by hand, I concentrated 5-50 mL of each sample using the Utermöhl settling method (Edler and Elbrächter 2010), depending on cell density. I analyzed samples under an inverted microscope (Zeiss Axiovert 35) with phase contrast within 48 h of the start of settling. Abundance data were based on the enumeration of representative sub-samples, according to the sampling procedures outlined in the UNESCO phytoplankton manual (Edler and Elbrächter 2010), with a minimum of 500 cells counted per sample. Empty cells were recorded, but not included in abundance counts. Diatoms were identified to the species level whenever possible, with taxonomy primarily based on Lebour (1930) and Tomas (1997); all names were verified with the most recent entries in the World Register of Marine Species (WoRMS, accessed May 2014). Flagellates were counted but not identified, as they contributed very little to the overall algal abundance in the Bering Sea (on average < 3% in the ice and the water).

After quantification by light microscopy, I processed a subset of ice algal samples with sufficient remaining biomass for more refined taxonomic analysis. I cleaned ten samples using a 1:1 ratio of 5.25% sodium hypochlorite and water to clear the organic material from the diatom frustules (Carr et al. 1986), then fixed a portion of each sample to a slide using Naphrax (Phycotech) with a refractive index of 1.73 (Hasle and Fryxell 1970). I then examined each sample under an inverted microscope (Zeiss Telaval 31). The remaining material was filtered onto a 0.8 µm Nuclepore filter and allowed to dry overnight, before being sputter-coated with gold and visualized using scanning electron microscopy with an electron microprobe (JEOL JXA-8530F). This non-quantitative species analysis was used to enhance the recorded diversity

of the ice algal community. Water and sediment trap samples were not reexamined, as there was insufficient biomass remaining in those samples.

Statistical analysis

Based on observations of vertical temperature gradients in the Bering Sea ice (Gradinger, unpublished data), I defined two time periods a priori: the period of ice growth and the period of ice melt (see above). This division was later confirmed through the analysis of multi-dimensional scaling plots based on various other environmental variables (see results, Fig. 3). Eight environmental variables were compared between the ice growth period and the ice melt period using two-sample t tests: ice thickness, ice concentration, snow depth, light intensity beneath the ice, surface salinity, and surface water concentrations of nitrate, phosphate and silicate. Primary ice type was compared between ice growth and ice melt periods using a one-way ANOVA.

To extrapolate species richness, I used EstimateS software (Colwell 2000) to create rarefaction curves with Chao 1 and Chao 2 bias-corrected formulas. This approach allowed for the prediction of the actual species richness in ice, water and sediment trap samples assuming a maximum of 100 samples in each of the three sample sets. To visualize differences in the species composition between the three sample sets, I created MDS plots based on Bray-Curtis similarity matrices using PRIMER E version 6 software. Because abundances among samples were of different orders of magnitude, I used relative species abundances (as % of total) to standardize the data across the three sample sets; samples were then divided between ice growth and ice melt periods.

To compare the overall species composition between the three sample sets, I performed a permutational multivariate ANOVA (PERMANOVA, Anderson 2001) using PRIMER. Comparisons were made separately for periods of ice growth and ice melt using relative species abundances. To determine the contribution of individual species to the differences between sample sets during each period, I used the similarity percentages routine (SIMPER) in PRIMER on relative species abundances; this allowed me to compile a list of those species that individually contributed 5% or more to the dissimilarity between any two sample sets. To compare the abundance of individual species among sample sets during each period, I performed

an ANOVA on relative species abundances from each period with sample type as the factor. The data were square-root transformed to meet assumptions of homoscedasticity; however, due to the high variability that is characteristic of biological data, one test still failed to meet the assumption (*Paralia sulcata*, Brown-Forsyth test, $p<0.05$).

I determined correlations among the community composition in the ice, water and traps using a Mantel's test (Mantel 1967) in the R package vegan. Correlations between seven environmental variables (ice concentration, primary ice type, ice thickness, snow depth, light levels beneath the ice, nutrient concentrations in the water, day length) and ice algal abundance, phytoplankton abundance, and vertical flux rates were made using PRIMER's BEST-BIOENV routine with 99 permutations.

I compared algal abundance and vertical flux rate between years and periods using two sample t-tests. Comparisons between years were conducted using only overlapping dates (April 4-28). Phytoplankton abundance was not included in this analysis as water samples were unavailable during April 2009. The relationships between cell counts and chlorophyll *a* concentrations in the sediment trap samples were determined using linear regressions for samples separately during ice growth and ice melt periods.

Results

Environmental conditions

The environmental conditions were distinctly different for the two selected periods of growing versus melting sea ice (Fig. 2). The ice growth period had significantly thicker ice, ranging from 0.50 to 1.00 m and averaging 0.82 m compared to 0.35 to 0.90 m, and a mean of 0.55 m for the melt period (t-test, $p<0.05$). The primary ice type also was significantly different between periods, with more white first year ice and young grey-white ice during ice growth compared to a wide range of ice types during the ice melt phase (ANOVA, $p<0.05$). The day length during ice growth was significantly shorter (t-test, $p<0.05$), ranging from 712 to 833 min with an average of 757 min before day 100 (ice growth) compared to 840 to 994 min with a mean of 903 min after day 100 (ice melt). The ice concentration and snow depth values were

slightly higher during ice growth, and the light intensities beneath the ice were slightly lower compared to ice melt conditions; however, none of these differences were significant (t-test, $p>0.05$ for all comparisons). There were no significant differences in surface water nutrient concentrations (nitrate, phosphate and silicate) or surface salinities between the ice growth and ice melt periods (t-test, $p>0.05$ for all comparisons).

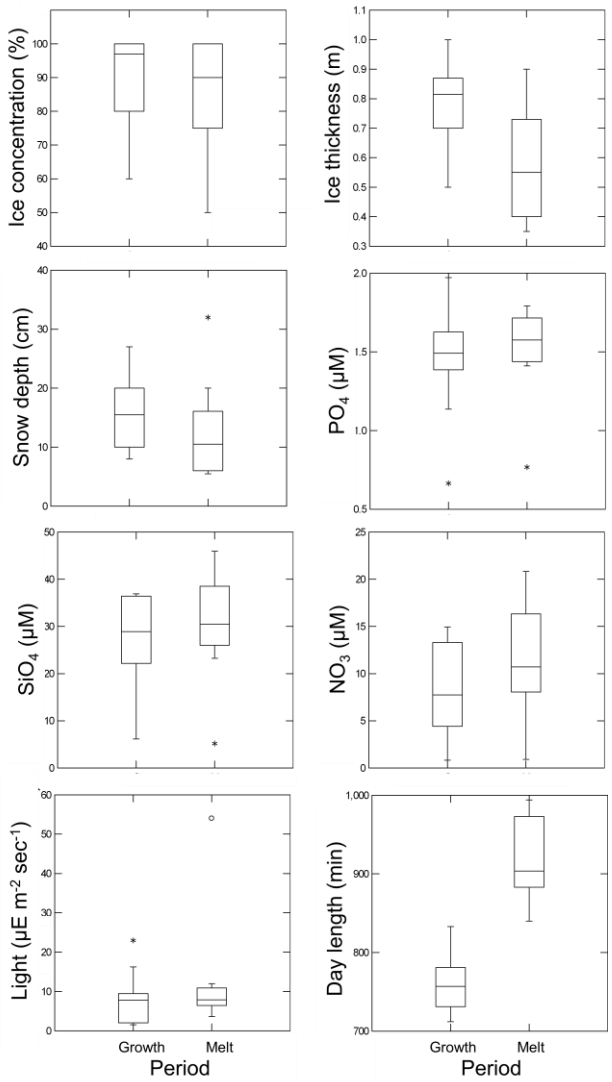

Figure 2. Environmental conditions at stations sampled during ice growth and ice melt periods. Phosphate (PO_4), silicate (SiO_4) and nitrate (NO_3) from the surface water.

A multidimensional scaling plot of the above environmental variables showed the clear separation in environmental conditions at stations sampled during the period of ice growth and the period of ice melt (Fig. 3).

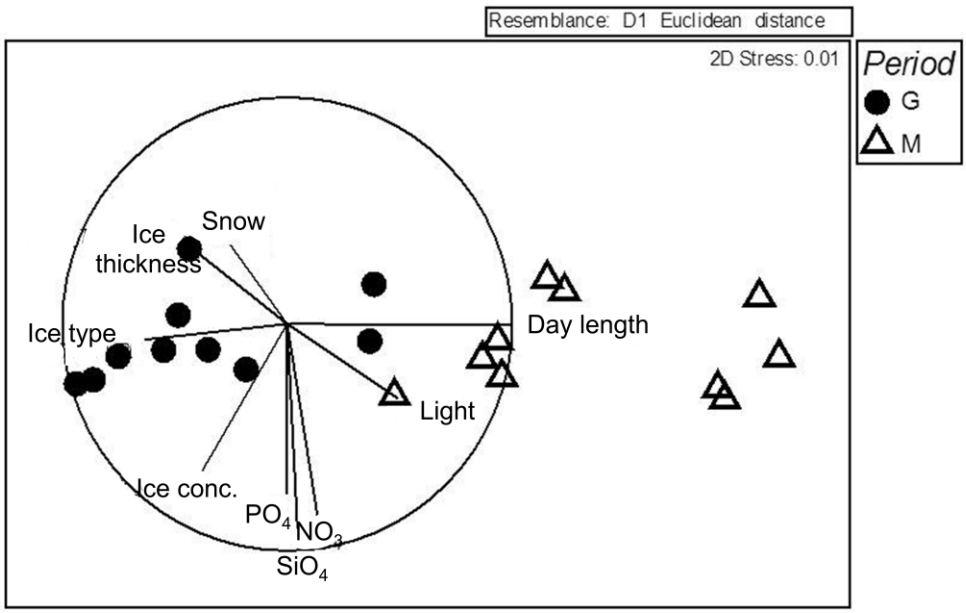

Figure 3. Multidimensional scaling plot based on the environmental conditions at stations sampled during ice growth and ice melt periods. Black circles indicate stations sampled during ice growth (G), open triangles indicate stations sampled during ice melt (M). A stress value of 0.01 indicates an excellent representation in two-dimensional space. *Conc.* concentration.

Diversity

Diatoms were the dominating group both in terms of abundances and species richness, within the limitations of the applied methodology. They dominated algal abundances in both ice and water, comprising 97% of ice algae and 98% of phytoplankton. A total of 74 diatom species were found: 71 in the ice, 36 in the water, and 42 in the sediment traps (Table 1). Fifty-one ice algal species could be distinguished using light microscopy, and were, therefore, used in

abundance and species composition analyses; the rest were added from SEM and cleaned sample analyses. Flagellates contributed less than 3% to total abundance in any sample set; because of my focus of cells > 20 µm and the limitations of my methodology, they were not identified.

Table 1. Diatom species inventory for Bering Sea ice, water and sediment trap samples. Bold indicates dominant species (contributing > 5% in at least one sample). "O" designates infrequent species appearing in two or fewer samples, "X" designates species appearing in more than two samples. "$" designates species found only through SEM.

Species	**Ice**	**Water**	**Traps**
Actinocyclus curvatulus	$		
Actinoptychus senarius			O
Amphiprora spp.	$		O
Attheya septentrionalis	$		
Bacteriosira bathyomphala	O		
Ceratoneis closterium	X	X	X
Chaetoceros radicans	$		
***Chaetoceros* spp.**	X	X	X
Chaetoceros sp. 1	$		
Cocconeis sp. 1		X	X
Cocconeis sp. 2			X
Coscinodiscus spp.	$	O	O
Coscinodiscus sp. 1	$		
Diploneis didyma	$		
Diploneis litoralis	$		
***Entomoneis* sp. 1**	X	X	X
Entomoneis sp. 2	X		O
Fallacia forcipata var. *densestriata*	$		
Fossula arctica	X	X	X
Fragilariopsis cylindrus	X	X	X
Fragilariopsis oceanica	X	X	X
***Gyrosigma* sp. 1**	X	X	X
Gyrosigma sp. 3	X	X	O
Gyrosigma tenuissimum var. *hyperborea*	$		
Haslea spp.	O		
Melosira arctica	O		
Navicula algida	X		
Navicula directa	X	X	X

Table 1, continued

Species	Ice	Water	Traps
Navicula kariana var. *detersa*	X		X
Navicula menisculus	$		
Navicula pelagica	O	X	
Navicula septentrionalis	X	O	X
Navicula sp. 1	$		
Navicula superba	O		
Navicula transitans var. *derasa*	$	O	
Navicula trigonocephala	O		
Navicula trigonocephala var. *depressa*	O	O	
Navicula valida	X	O	O
Navicula vanhoeffenii	X		X
Nitzschia angulata	$		
Nitzschia pellucida	X	X	X
Nitzschia frigida	X	X	X
Nitzschia lanceolata	$		
Nitzschia sigma	X	O	X
Nitzschia sp. 1	X	O	X
Nitzschia sp. 2	X	O	X
Odontella aurita	O		O
Paralia sulcata	O	X	X
Pauliella taeniata	X	X	X
Pinnularia quadratarea var. *bicontracta*	X		O
Pinnularia quadratarea var. *capitata*	O		
Pinnularia quadratarea var. *constricta*	X	O	X
Pinnularia quadratarea var. *cuneata*	O		
Pinnularia quadratarea var. *densestriata*	O		O
Pinnularia quadratarea var. *dubia*	X		O
Pinnularia sp. 1	O		
Pinnularia sp. 2	O		
Pinnularia sp. 3	O		
Pinnularia sp. 4	X	X	O
Pinnularia sp. *5*	O	O	
Plagiotropis spp.	$		
Pleurosigma spp.	X	O	X
Pleurosigma teuniforme	O	X	X
Pseudogomphonema arctica	$		
Pseudogomphonema groenlandicum	X	O	O

Table 1, continued

Species, continued	**Ice**	**Water**	**Traps**
Pseudogomphonema septentrionale	X	X	X
Pseudogomphonema septentrionale var. *angustatum*	$		
Pseudo-nitzschia delicatissima	X	X	X
Pseudo-nitzschia seriata	X	X	X
Stenoneis inconspicua	O		
Thalassionema nitzschioides	O	X	X
Thalassiosira hyalina	X	X	X
Thalassiosira nordenskioeldii	$	O	O
Thalassiosira spp.	X	X	X
Unidentified flagellates	X	O	X

Only 15 of the 57 species quantified using light microscopy contributed more than 5% to the total abundance in any one sample and were considered "abundant" (Table 1). Of the remaining species, 11 were very rare and appeared in one or two samples only. The algal abundances in ice, water and sediment trap samples were all dominated by *Fragilariopsis* spp. with 28%, 37% and 52%, respectively. All of the abundant and frequently occurring species (those found in over 50% of the samples by sample set) were found within all three sample sets. No numerically important species was associated exclusively with ice, water or sediment trap samples.

Rarefaction curves were used to extrapolate the actual species richness in each sample set (Fig. 4). Species richness in the ice was estimated at 63 species maximum, reached at 80 samples, while in the water and sediment traps the asymptote was reached at 50 samples, with a total of 43 species in the water and 48 in the traps. Including the species identified from the ice based on the SEM and cleaned sample analysis, the estimation of species richness in ice increased to 82 at 80 samples.

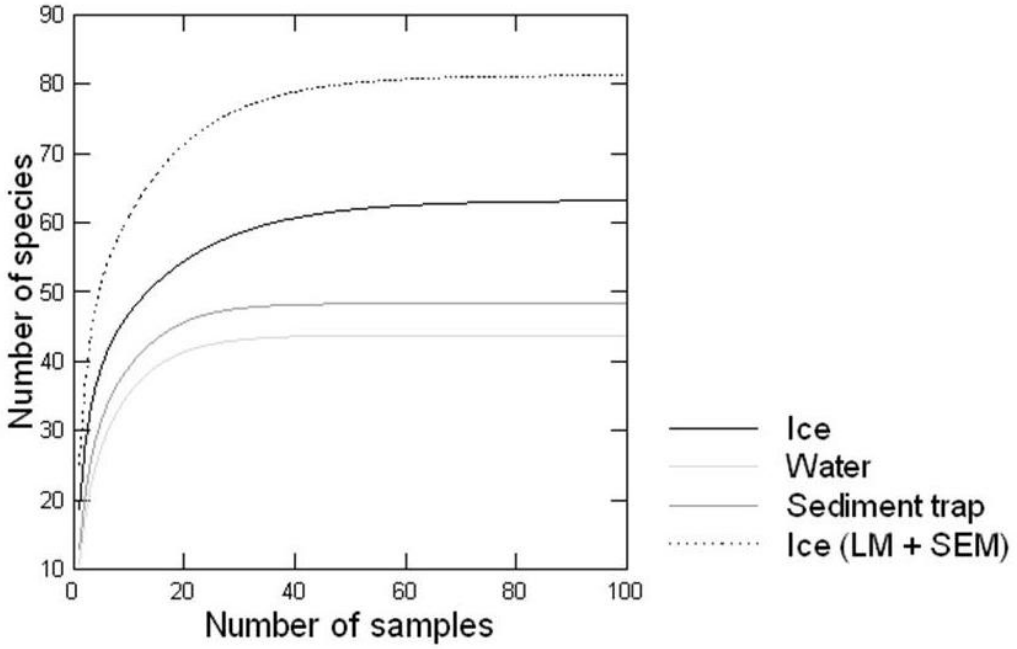

Figure 4. Rarefaction curves showing extrapolated species richness in ice, water and sediment trap samples given 100 samples. Solids lines indicate species richness based on light microscope analysis (ice samples n=20, water samples n=13, sediment trap samples n=20). Dotted line indicates species richness based on light microscope (LM) and scanning electron microscope (SEM) analysis (ice samples n=10).

Abundance and vertical flux rate

The abundance of ice algae (Table 2) increased significantly between the ice growth and the ice melt periods (t-test, $p<0.05$). During ice growth, ice algal abundance ranged from 1.86 x 10^4 to 7.40 x 10^7 cells l^{-1}, with an average of 1.56 x 10^7 cells l^{-1}; during ice melt, ice algal abundance ranged from 1.17 x 10^7 to 1.39 x 10^8 cells l^{-1}, with an average of 5.85 x 10^7 cells l^{-1}. Ice algal abundance was not significantly correlated to either day length or day of the year ($p>0.05$). Abundances in the ice were significantly higher than those in the water (t-test, $p<0.05$); on average, ice algal abundance was three orders of magnitude higher than that of the phytoplankton. Phytoplankton abundance did not change significantly between periods (t-test, $p>0.05$) but was highly variable among stations, ranging from 4.00 x 10^2 to 6.50 x 10^4 cells l^{-1}, with an overall average of 1.29 x 10^4 cells l^{-1} across both periods. The vertical flux beneath the

ice was significantly higher during ice melt compared to ice growth (t-test, $p<0.05$). During ice growth, flux rates ranged from 3.63×10^5 to 1.39×10^8 cells m^{-2} day^{-1}, with an average of 4.16×10^7 cells m^{-2} day^{-1}; during ice melt, flux rates ranged from 1.08×10^7 to 3.67×10^8 cells m^{-2} day^{-1}, with an average of 1.19×10^8 cells m^{-2} day^{-1}. There was no significant difference in ice algal abundance or vertical flux rate between years ($p>0.05$ for both comparisons). Comparisons of phytoplankton abundance could not be made as water sampling dates did not overlap between years.

Table 2. Mean algal characteristics during ice growth and ice melt periods. Mean algal abundance in ice and water samples (cells l^{-1}) and mean vertical flux rate beneath the ice (cells m^{-2} day^{-1}) during ice growth and ice melt periods. Coefficient of variation (CV=SD/mean) reported as percent of the mean. Mean standing stock (*S.S.*) in the ice (cells m^{-2} in the bottom 2 cm) and the water (cells m^{-2} in the upper 5 m) during ice growth and ice melt periods, as well as mean percent of the standing stock sinking per day (*% S.S. sinking* day^{-1}). Proportion of abundance comprised of empty cells in each sample set during ice growth and ice melt periods. Chlorophyll *a* concentrations (µg chl-*a* m^{-2} for ice and water) and flux rate (mg chl-*a* m^{-2} day^{-1} for traps), and estimated chl-*a* $cell^{-1}$ within each sample set during ice growth and ice melt periods.

Ice growth

	Mean cells	CV%	Mean S.S.	% S.S. sinking day^{-1}	% Empty cells	Chl-a*	pg Chl-a $cell^{-1}$*
Ice	1.56×10^7	158.09	3.46×10^8	75.94	0.91	113.01	6.05
Water	5.72×10^3	141.79	3.47×10^7	202.01	17.41	0.14	23.08
Traps	4.16×10^7	131.93	--	--	19.23	1.10	32.51

Ice melt

	Mean cells	CV%	Mean S.S.	% S.S. sinking day^{-1}	% Empty cells	Chl-*a* *	pg Chl-*a* $cell^{-1}$*
Ice	5.85×10^7	85.97	1.17×10^9	21.7	0.05	432.23	7.39
Water	2.45×10^4	99.83	1.22×10^8	368.06	0.76	0.61	25.12
Traps	1.20×10^8	112.94	--	--	3.91	3.08	25.76

* Chlorophyll *a* concentrations courtesy of R. Gradinger, unpublished data.

During the ice growth period, the vertical flux represented the sinking of an average of 76% of the ice algal standing stock in the bottom 2 cm per day, or an average of over 200% of the phytoplankton standing stock in the upper 5 m of the water column, assuming that the phytoplankton abundance throughout the upper 5 m was the same as measured at 5 m depth, and assuming a 100% contribution to the flux of cells from either the ice or the water (Table 2). During the ice melt period, the vertical flux rate represented the sinking of 22% of the ice algal standing stock or 368% of the phytoplankton standing stock. These proportions were highly variable by station, ranging from <1 to 150% of the ice algae and 10 to 1500% of the phytoplankton across both periods. The proportions for ice algae and phytoplankton, respectively, did not differ significantly between ice growth and melt periods (t-test, $p>0.05$ for both comparisons), nor did they differ between years (t-test, $p>0.05$ for both comparisons).

There was no significant correlation between ice algal abundance, phytoplankton abundance, or vertical flux rate and the environmental variables measured (ice concentration, primary ice type, ice thickness, snow depth, nutrient concentrations in the water, and day length) during either ice growth or ice melt periods (BEST-BIOENV, $p>0.05$ for all comparisons).

Fate of ice algae

During ice growth, the species composition in the ice was significantly different from that in the water and the traps based on relative species abundances (PERMANOVA, $p<0.05$ for both comparisons). There was no difference in the composition in the water and the traps during ice growth or ice melt (PERMANOVA, $p>0.05$ for both comparisons). However, during ice melt, the composition in the ice and the water were no longer significantly different (PERMANOVA, $p>0.05$) while the ice algal composition remained different from that found in the trap samples (PERMANOVA, $p<0.05$). When the species compositions were visualized using an MDS plot, these differences could be seen among sample sets (Fig. 5); the stress values indicate a reasonably good representation of the data in two dimensional space (Clarke 1993).

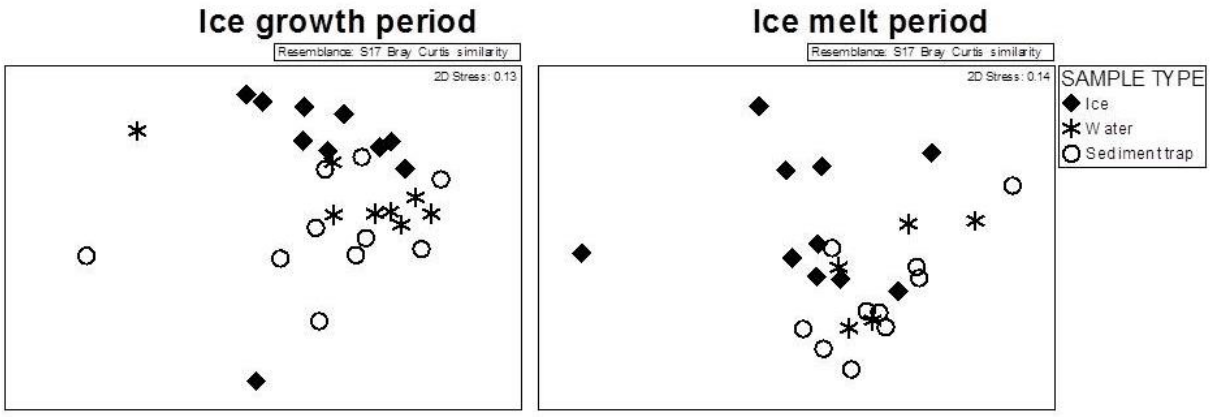

Figure 5. Multi-dimensional scaling plots of the relative species abundance (as % of total) in ice, water and sediment trap samples. Left panel shows similarity of samples during the period of ice growth, right panel shows similarity of samples during the period of ice melt.

Only six species were individually responsible for 5% or more of the dissimilarity in community composition between sample sets based on SIMPER analyses, and, therefore, were used for comparisons between sample sets. During ice growth, these species included *Fragilariopsis* spp., *Nitzschia frigida, Paralia sulcata* and *Chaetoceros* spp., which together contributed to over half of the difference among sample sets (SIMPER, 57%). During melt, the same species were important with the exception of *Chaetoceros* spp., while *Pauliella taeniata* and *Fossula arctica* also contributed substantially; together these five species were responsible for 72% of the difference among sample sets.

When the relative proportions of the key species identified as driving the dissimilarity among sample sets were individually compared between ice, water and traps, I found several differences (Fig. 6). During the ice growth period, there were significantly higher proportions of *Chaetoceros* spp. and *Paralia sulcata* in the water and traps as compared to the ice (ANOVA, $p<0.05$ for both comparisons); when all centric diatoms were grouped, there were significantly higher proportions in the water and traps than in the ice (ANOVA, $p<0.05$ for both comparisons). There were also significantly lower proportions of *Nitzschia frigida* in the water and traps as compared to in the ice during the ice growth period (ANOVA, $p<0.05$). During the ice melt

period, once again there were significantly higher proportions of centric diatoms and lower proportions of *N. frigida* in the water and traps when compared to the ice (ANOVA, $p<0.05$ for all comparisons). There were also significantly higher proportions of those diatoms forming ribbon-colonies (i.e., *Fragilariopsis* spp., *Fossula arctica, Pauliella taeniata*) in the traps than in the ice (ANOVA, $p<0.05$).

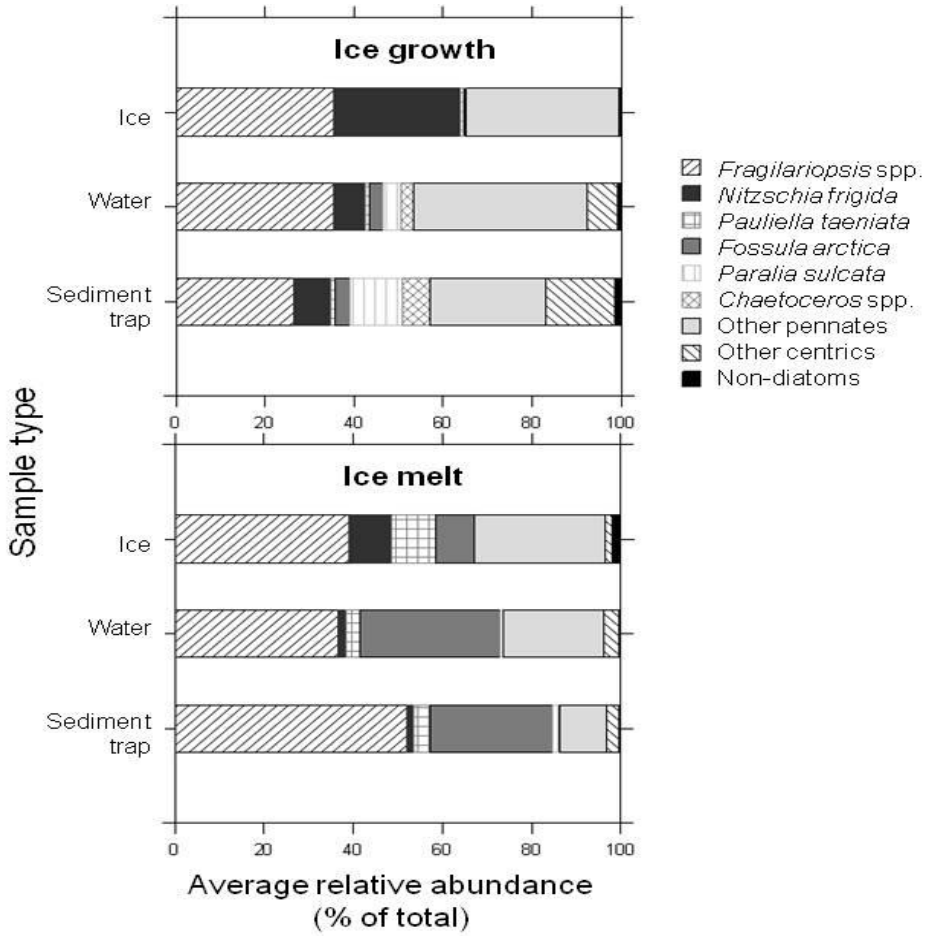

Figure 6. Relative abundance (% of total) of species in ice, water and sediment trap samples. Species shown are those contributing >5% to the dissimilarity between sample sets based on SIMPER analysis. Upper section shows species composition during the ice growth period, lower section shows species composition during the ice melt period.

I looked for correlations in the proportion of dominant species between sample sets using a Mantel's test. During both periods, the species composition in the water and the traps was significantly correlated ($r=0.30$, $r=0.34$, for ice growth and ice melt, respectively; $p<0.05$ for both correlations). During ice melt, the composition in the ice and the water was also significantly correlated ($r=0.41$, $p<0.05$). No other correlations between sample sets were significant.

Discussion

I present the first quantitative assessment of the Bering Sea ice algal community composition and the first direct examination of the connection between algal communities from the ice and water and vertical flux beneath the ice in this region. This study showed a highly abundant and diverse ice algal community, coupled with a very similar phytoplankton community that remained at low abundances throughout the spring. The similarity of species between ice and water is also reflected in the composition of the sediment traps, which captured a substantial vertical flux of cells even in early spring. I will first discuss the environmental conditions found during the course of this study, which occurred during a cold period in the Bering Sea. Secondly, I will describe the diversity in the ice, water and sediment traps in comparison to other subarctic and Arctic regions. Thirdly, I will compare the abundance of cells in these sample sets and describe how they changed between ice growth and ice melt periods in the spring. And finally, I will discuss the vertical flux of cells beneath the ice in the context of the ultimate fate of ice algae in the Bering Sea.

Environmental conditions

The environmental conditions in the Bering Sea were significantly different during the periods I defined as ice growth and ice melt, revealing a transition from thick first-year ice in the early spring to thinner, more variable ice types from mid-April to May. Throughout both periods the conditions reflected the cold climate and heavy ice cover in the Bering Sea during 2008 and

2009 (Wendler et al. 2013). Ice cover was extensive at all stations sampled, with only two stations displaying less than 75% coverage. Although ice thickness significantly decreased from the period of ice growth to ice melt, it remained substantial throughout the spring with a minimum of 0.40 m; it should be noted that this may also reflect the non-random nature of station selection, which favored thick, stable ice floes for safety reasons and, therefore, may not be fully representative of the entire region. The thick ice coupled with undiminished snow cover resulted in low light levels under the ice, averaging 10 μmol m^{-2} sec^{-1}, which approached the minimum for ice algal growth (~1 μmol m^{-2} sec^{-1}; Mock and Gradinger 1999). Surface water temperatures were near freezing throughout the spring. The maximum ice extents during 2008 and 2009 were among the greatest since the 1970's, extending south of St. Paul Island and reaching a maximum in the southern Bering Sea at the end of March (Sigler and Harvey 2010). These characteristics made the Bering Sea essentially an Arctic system during the spring.

Our sampling occurred during a recent cold period in the Bering Sea which started in 2007, characterized by extensive sea ice extent and late ice melt. The five years prior (2001-2005) were warm, with low ice extent in the spring and earlier ice retreat by as much as six weeks (Overland et al. 2009; Stabeno et al. 2012b). These regular fluctuations in Bering Sea ice and water conditions are primarily the result of shifts in wind direction during the spring. During cold years, strong northerly winds draw cold Arctic air into the Bering Sea, delaying ice melt and causing ice to be advected farther south across the shelf; during warm years, weaker easterly winds bring in warmer air and fail to maintain ice on the southern shelf regions (Stabeno et al. 2012b). Currents also differ between cold and warm years, with westward currents during the former bringing cold coastal water across the shelf, while a more northward flow during the latter draws up warmer water from the Alaska Peninsula (Stabeno et al. 2012b).

The conditions in the Bering Sea during this study were similar to those found in other subarctic seas, e.g., the Sea of Okhotsk on the Pacific side and the Labrador and Barents seas on the Atlantic side. These regions are transition zones between Arctic and temperate climates, and are characterized by locally formed first-year ice 1-2 m thick, which reaches its maximum extent in March, then completely retreats during the ice-free summer months (Wang et al. 2007). In the spring this creates a highly dynamic ice-edge zone that can be very productive. Compared to other subarctic regions, the Bering Sea has high nutrient concentrations in the water due to the

input of nutrient-rich water from the Gulf of Anadyr and, to a lesser extent, the Gulf of Alaska (Loughlin and Ohtani 1999). The Bering Sea shelf is also shallower than most other subarctic seas (Wang et al. 2007), allowing for the close coupling between benthic and pelagic realms (Grebmeier 1988).

Ice conditions in the high Arctic are quite different from those in the subarctic Bering Sea, with near-constant ice cover in many areas and a significant proportion of multi-year ice (Thomas and Dieckmann 2003); recently, the Arctic has seen a dramatic decline in sea ice extent, unlike in the Bering Sea where ice extent has not significantly changed over the past decades (Brown and Arrigo 2012). This stability in Bering Sea ice is due to its wind-driven ice formation, by which strong northerly wind causes a "conveyor belt" of ice formed in the northern coastal regions and that is then advected south over the shelf (Pease 1980). Although there is high inter-annual variation in winter winds, there has been no major shift in wind direction over the past decades (Brown and Arrigo 2012). However, the recent increase in Arctic winter air temperatures, which results in a warmer northerly wind, may ultimately affect ice formation in the Bering Sea, as Bering Sea ice formation is driven by atmospheric processes in the Arctic.

Diversity of ice algae and phytoplankton

Traditionally, diversity in the Arctic flora and fauna was believed to be quite low relative to temperate and tropical regions, due to the harsh climate and comparative instability of environmental conditions (Sanders 1968). However, recent studies show that among marine microalgae the diversity in the Arctic is in fact higher than predicted. In a recent inventory, Poulin et al. (2011) compiled a list of 2106 algal species in the Arctic (1027 in the ice, 1874 in the water), which is a large number considering a current inventory of only approximately 5,000 phytoplankton species worldwide (Tett and Barton 1995).

The recent compilation of ice algal and phytoplankton diversity underscored another important aspect of Arctic algal diversity, which is the regional disparity of investigations. Some regions (e.g., Hudson Bay, the Norwegian Barents Sea, the Beaufort and Chukchi seas) have been thoroughly explored, with each region subject to over a dozen studies documenting algal diversity, while other Arctic and subarctic regions remained virtually unexamined. The Bering

Sea is one such notable case. Only a sparse handful of surveys have investigated the diversity of Bering Sea phytoplankton, and aside from the limited examination of two ice cores taken in the 1970's (Schandelmeier and Alexander 1979), to date there has been no description ice algal diversity in the Bering Sea.

The diversity that I found in the Bering Sea ice algae was much higher than these limited earlier investigations suggested. In addition to the 15 species from those surveys (with the exception of *Ditylum brightwellii* and *Actinoptychus undulatus*; Schandelmeier and Alexander 1979), I found 58 others that have never before been recorded in the Bering Sea (Table 1). This large increase in species richness is due to the ten-fold higher number of samples processed, and the addition of scanning electron microscopy in this study, which increased my species inventory by a third compared with traditional light microscopy alone. Extrapolations of species richness using a rarefaction curve further increased this number to a final estimate of 82 species (Fig. 4).

A recent study applied molecular techniques to ice algal communities in the Bering Sea, with a focus to assess zooplankton grazing pressure rather than diversity in the winter/spring of 2010 (Durbin and Casas 2014). Unfortunately, loss of samples forced the authors to use Lugols-fixed algae, which are not ideal for molecular analysis; they identified less than a third of the number of diatom species found in this study (23 vs. 71, Durbin and Casas 2014). Interestingly, eleven of these were not identified in my study; while there may have been differences in the community composition between years, many of these species were among those taxa identified in my study only to genus (e.g., *Navicula* spp., *Nitzschia* spp.), suggesting that molecular techniques could be useful for further enhancing our understanding of Bering Sea algal diversity.

The inventory by Durbin and Casas (2014) also included several non-diatom ice algae including two dinoflagellates, a cryptophyte, and five cercozoans, whereas I focused solely on diatom species >20 µm and excluded the identification of any flagellate species, as morphological taxonomy using light microscopy is most accurate for this size class of diatom taxa. A recent review suggested that in the Alaskan Arctic small cells (<20 µm) contribute on average only 4% to the species richness of ice algae, and flagellates contribute less than 10% (Poulin et al. 2011).

The diversity of ice algae across the Arctic is highly variable and likely still under-sampled; with 71 species, the observed species richness of diatoms in the Bering Sea ice in this

study was higher than the species richness of diatoms in the Kara Sea (11 species; Druzhkov et al. 2001), the Laptev Sea (19 species; Tuschling et al. 2000) and the Arctic Ocean (25 species; Booth and Horner 1997), but lower than in the East Siberian Sea (115 species; Okolodkov 1993), the Canadian Arctic (197 species; Hsiao 1983), and the Chukchi Sea (251 species; von Quillfeldt et al. 2003). It should be noted, however, that species richness estimates depend greatly on the sampling effort and the methodology of identification, as demonstrated in this study where species richness increased substantially in the ice when a) extrapolated over a higher number of samples and b) analyzed with the addition of scanning electron microscopy (Fig. 4). Therefore, caution should be used when comparing species richness across studies.

The Bering Sea ice algal community was composed of both polar and polar/temperate species, but was more similar to ice algal communities in Arctic regions than to other subarctic seas. In the Okhotsk Sea—a subarctic sea that lacks the Bering Sea's Arctic connection—the spring sea ice is overwhelmingly dominated by centric diatoms common to the Pacific (e.g. *Odontella aurita*, *Thalassiosira punctigera*, *Detonula confervacea;* McMinn et al. 2008), which were rare or absent in the Bering Sea. The brackish Baltic Sea has a more similar community of polar diatoms through its relic connection to the Arctic, but the dominant Bering Sea taxa (i.e., *Fragilariopsis* spp.) is not common there (Ikavalko and Thomsen 1997; Haecky et al. 1998). The Barents Sea also shares many polar species with the Bering Sea, but its dominant species (i.e., *Nitzschia pomare*, *Synedropsis hyperborea*, and *Chaetoceros* spp.; Falk-Petersen and Sargent 1998; Hegseth 1998) only rarely appeared in Bering Sea ice. The high abundance of *Nitzschia frigida* and *Fragilariopsis* spp. in the Bering Sea is characteristic of many Arctic regions, including the Beaufort Sea (Horner and Schrader 1982), the Canadian Arctic (Fortier et al. 2002; Melnikov et al. 2002; Tremblay et al. 2006), and the Norwegian Sea (McMinn and Hegseth 2004; Leu et al. 2010). However, there was one major difference between Bering Sea and other Arctic ice algae: the near-absence of *Melosira arctica*, a chain-forming centric diatom primarily found on multi-year ice that is ubiquitous in nearly all Arctic regions, and can contribute a substantial amount to the overall biomass of Arctic ice algal communities (e.g. Poulin et al. 2014). It should be noted that *M. arctica* was found in high abundance during a BEST cruise in Bering Sea in May/June 2010, suggesting possible seasonal or interannual variability in its occurrence in this region (Wang et al. 2014). The Bering Sea also appears to lack the ice-

associated amphipods that are endemic to the Arctic (K. Iken, unpublished data), and are a major part of the sympagic food web there (Iken et al. 2005).

Among the phytoplankton, I found a subset of the same species as in the ice, but there was lower species richness in the water at every station. Many previous studies have found similarly lower diversity in the sub-ice phytoplankton as compared to the overlying ice (e.g., Margalef 1977; Horner 1985; Hsiao 1992). With a total of 36 species, the species richness of diatoms in the Bering Sea phytoplankton was higher than found beneath the ice during the spring in the Kara Sea (8 species; Druzhkov et al. 2001) and the Arctic Ocean (30 species; Booth and Horner 1997), but lower than in northern Baffin Bay (70 species; Lovejoy et al. 2002); although again, comparisons should be made with caution due to the differences in sampling effort and methodology. Studies covering different time spans also make comparisons difficult, as phytoplankton communities undergo extensive seasonal succession, and annual species richness at a single location can exceed 240 species (e.g., Hsaio 1983).

The very high similarity between the sea ice and phytoplankton algal species indicated that the spring phytoplankton originated from the ice, as only one (*Cocconeis* sp. 1) of the 36 species found in the water was not also present in the ice. A 1977 survey of the Bering Sea phytoplankton (Schandelmeier and Alexander 1979) found similar species in March to those in this study, although they recorded only 12 species. More recent work has also noted the presence of common ice species (e.g. *Fragilariopsis* spp., *Nitzschia* spp.) in the sub-ice phytoplankton in the Bering Sea (Sherr et al. 2013). The duality of ice algal and phytoplankton species is recurring: because many subarctic and Arctic regions including the Bering Sea are ice-free in the summer, new sea ice must be seeded with biota from existing phytoplankton populations (Ikavalko and Gradinger 1998; Riedel et al. 2007). Organisms are incorporated into the ice during its earliest formation stages, scavenged from the water by rising frazil ice (Ikavalko and Gradinger 1998), or lifted from the benthos by deep-forming frazil or anchor ice (Reimnitz 1992; Reimnitz and Clayton 1993). There are few truly endemic ice algal species in the Arctic (e.g., *Nitzschia frigida*, *N. promare*, *Melosira arctica*; Ambrose et al. 2005; Poulin et al. 2011) and of these, only *N. frigida* is abundant in the Bering Sea. *N. frigida* has previously been recorded among Arctic phytoplankton (e.g., Booth 1984; Druzhkov et al. 2001), but always as a remnant from the ice. *Fragilariopsis cylindrus*, another dominant species among the Bering Sea ice algae,

has long been used as a paleo-indicator of sea ice; however, it has been found in the water column in entirely ice free areas (von Quillfeldt 2004, and references therein) and thus is more accurately viewed as a cold water species.

The species composition of the Bering Sea phytoplankton was unique from other Arctic spring phytoplankton communities in its degree of similarity to the ice algal community, a similarity that appears to vary in space and time. Spring phytoplankton communities in the Bering Sea vary considerably across the shelf, with the dominance of ice algal species increasing with increased proximity to the ice edge (Schandelmeier and Alexander 1981). The similarity to ice algal communities is short-lived, and by late spring/early summer the phytoplankton composition in the Bering Sea shifts to a more centric-dominated community (Taniguchi et al. 1976). Ice-associated species are replaced by pelagic centric diatoms such as *Thalassiosira nordenskioeldii* and *T. decipiens*, which were rare or absent during this study, although some pennate species (e.g. *Fossula arctica, Navicula* spp.) continue to be found in high abundance in some parts of the water column (Taniguchi et al. 1976). This transition is typical of subarctic and Arctic phytoplankton (e.g. Michel et al. 1997; Haecky et al. 1998; Tamelander and Heiskanen 2004), which classically undergo a succession from the chain-forming pennate species that dominate the ice algae, followed by a more centric-dominated community later in the season (von Quillfeldt 2000). However, even in other early-stage Arctic phytoplankton communities (Legendre et al. 1981; Horner and Schrader 1982; Haecky et al. 1998) none matched the degree of overlap between the ice algal and phytoplankton species as in the Bering Sea in this study.

In the sediment trap samples, the species composition was very similar to that found in both ice and water. Of the 42 species that were identified from the traps, all but two were present in the ice—*Actinoptychus undulatus* and *Cocconeis costata*—each of which was found only once as a single individual. *A. undulatus* was previously recorded in Bering Sea ice (Schandelmeier and Alexander 1979) so it may have occurred there in low abundance in this study, while *C. costata* may have been advected from elsewhere on the shelf, or possibly resuspended from the shallow sediments. Over three-quarters of the rare ice algal species (those appearing only in one or two samples) did not appear in the traps, suggesting that the short (4-6 hour) deployment time may not have been sufficient to capture the rare species. However, as all abundant species were

found throughout all three sample sets, there appears to be no strong separation between the ice, water and vertical flux in terms of species inventories during the spring.

Abundance of ice algae and phytoplankton

The abundance of ice algae in the Bering Sea was very high throughout the entire spring sampling period, so ice algal production must begin before mid-March. Abundance increased from the period of ice growth to the period of ice melt; however, there was no significant relationship between any physical factors measured in this study and the abundance of ice algae. The absence of a clear relationship between environmental variables and abundance may be due to the high variability in both data sets, as observed previously in the Chukchi Sea, where no relationship was found between ice algal coverage and any large scale environmental variable (Ambrose et al. 2005). It is also possible that other factors influenced ice algal abundance that were not measured in this study, such as sub-ice topography (Melnikov 1987), rate of ice growth and melt (Legendre et al. 1991), distance from the edge of the ice floe (Ambrose et al. 2005), or the local ice conditions in the days prior to sampling.

The abundance of ice algae during ice melt was among the highest reported in both subarctic and Arctic regions, although abundances at individual stations from the Canadian Arctic and the Beaufort Sea surpassed even the highest abundance found in this study (Hsiao 1980; Horner and Schrader 1982). Those stations were sampled during late May, and ice algal abundances in the Bering Sea may have been similarly high that late in the spring. The high abundance in the Bering Sea ice may be due to the nutrient-rich underlying water, which is higher than in most other subarctic and Arctic seas (e.g., Gradinger 2009).

Phytoplankton abundance was very low throughout both spring periods, and did not significantly increase from the period of ice growth to ice melt. Abundance was three orders of magnitude below levels previously recorded on the Bering Sea shelf in May (Taniguchi et al. 1976). Although the spring ice-edge phytoplankton bloom typically begins the last week in April in the Bering Sea (Sigler et al. 2014), the cold springs in 2008 and 2009 retarded the development of the bloom, postponing it until late May and early June based on chlorophyll *a* concentrations (Sherr et al. 2013). The key drivers of phytoplankton blooms in subarctic and

Arctic seas are 1) sufficient light for algal growth, and 2) sufficient stratification to maintain cells above the 1% PAR level, both of which are accomplished during ice retreat (Legendre et al. 1981). However, the ice did not retreat substantially during the periods that were sampled during this study. Throughout the spring the mixed layer depth remained well below the 1% PAR level, which was shallow due to thick ice and snow cover (Fig. 7; M. Lomas, unpublished data). The consistently high surface salinity during both ice growth and ice melt periods indicated that there was insufficient melt water to drive any strong density-dependent stratification in the water column, and the lack of change in surface nutrient concentrations between ice growth and ice melt periods confirms that the phytoplankton bloom had not yet occurred.

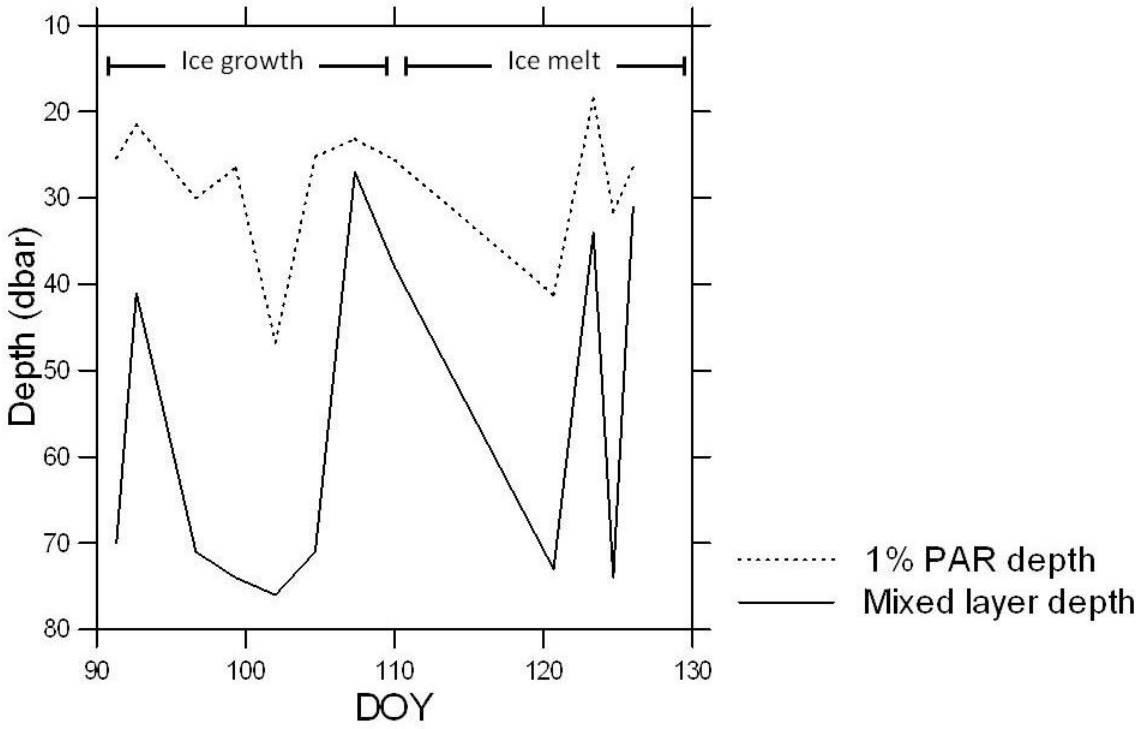

Figure 7. Comparison of the euphotic zone (as indicated by the 1% PAR depth) and the mixed layer depth in the Bering Sea during ice growth and ice melt periods in 2008 and 2009 (M. Lomas, unpublished data).

In some Arctic regions, large phytoplankton blooms have been found under full ice cover, which can match or even exceed spring phytoplankton bloom chlorophyll *a* concentrations (e.g., Gradinger 1996, Fortier et al. 2002, Arrigo et al. 2012, Arrigo et al. 2014). I found no evidence for this phenomenon in this study. One key difference is that regions with large under-ice phytoplankton blooms are all characterized by extensive coverage of melt ponds on the surface of the ice. Melt ponds allow approximately four times the light penetration as compared to bare ice (Arrigo et al. 2012), while snow covered ice allows even less light to reach the underlying water. No melt ponds were recorded around the stations sampled in the Bering Sea during this study, and snow cover was consistently thick, preventing the sufficient penetration of light beneath the ice that would be required to support such large under-ice phytoplankton blooms.

Vertical flux of algal cells

There was a large vertical flux of algal cells beneath the ice throughout the spring, which increased significantly during the ice melt period. Prior to ice melt, most seasonally ice-covered regions have minimal vertical flux under the ice (e.g., Bauerfeind 1994; Michel et al. 1997; Olli et al. 2002); however, there can be high variability in the timing and intensity of flux depending on meteorological conditions (Fortier et al. 2002; Michel et al. 2006). The high vertical flux rate and low phytoplankton abundance during ice growth in the Bering Sea indicated that there was an input of cells from the ice into the water prior to ice melt. The observed vertical flux would have required on average the sinking of over 200% of the phytoplankton standing stock in the upper 5 m per day to support it. As phytoplankton growth rates in the Bering Sea during ice growth are low ($< 0.1\ d^{-1}$; Moran et al. 2012), such high flux rates would quickly exhaust the standing stock without input from another source. During the ice growth period, the ice algal standing stock in the bottom 2 cm of sea ice alone was on average several times the size of the phytoplankton standing stock in the upper 5 m, so the release of cells from this domain could more easily support the observed flux rates.

During the ice growth period, the release of ice algal cells likely resulted from periodic ablation of the fragile bottom layer of the ice, which contains the bulk of the ice algal biomass.

Ice algae can be present in a loosely attached under-ice film (Ambrose et al. 2005), so slight melting from the heat flux from tidal flow or ocean swells could easily dislodge cells (Pogson et al. 2011). The accumulation of ice algae and subsequent conversion of solar radiation into heat has also been shown to cause local melting of the ice, resulting in the release of ice algae into the water (Zeebe et al. 1996). Such sporadic release would explain the high variability in flux rates that I found among stations. The release of dead algal cells from the ice through brine drainage could also contribute to the vertical flux, and would explain the relatively higher proportion of empty diatom frustules found in the trap samples compared to the ice (Table 2). These empty frustules in the ice result from microzooplankton grazing, which was high in the Bering Sea at the time of this study (Sherr et al. 2013), and also from parasitism by chytrids, which was observed in the ice at several stations (A. Szymanski, unpublished data).

The early spring vertical flux of cells is an important source of food for benthic organisms. The shallow Bering Sea shelf has tight pelagic-benthic coupling that supports large benthic communities (Grebmeier 1988). Sediment oxygen uptake under full ice cover in March showed significant metabolic activity of benthic organisms, indicating that the Bering Sea benthos has an active community even in early spring (Cooper et al. 2013). This activity is likely supported by the vertical flux of algae; flux rates of chlorophyll *a* in March were consistent with inventories of chlorophyll *a* extracted from surface sediments, which showed accumulations of up to 20 mg m^{-2} (Cooper et al. 2013). The large amount of chlorophyll *a* in the surface sediments supports my observations that the majority of material sinking from the ice was in the form of "fresh" algal cells. In general, primary production is modified during its export from surface to benthos, and vertical flux can be composed of ungrazed algae, organic debris (e.g., empty frustules, detritus), and fecal pellets from zooplankton (e.g., Fortier et al. 1994). The contribution of fecal pellets can be up to 99% of the overall marine flux depending on season and region (Lampitt et al. 1990), but under the ice in this study they appeared only rarely. Empty diatom frustules contributed less than 20% to the overall flux of cells during ice growth, and only 3% during ice melt. Thus the majority of algal production sinking from the ice goes directly to the benthos without being reworked through the pelagic system, making it a high quality food source.

In order to make comprehensive regional comparisons of vertical flux rates, I included chlorophyll measurements from ice, water and sediment traps conducted within the BEST program (R. Gradinger, unpublished data). The vertical pigment flux averaged 1.10 mg chlorophyll *a* m^{-2} day^{-1} during ice growth and 3.08 mg chlorophyll *a* m^{-2} day^{-1} during ice melt (Table 2; R. Gradinger, unpublished data); pigment fluxes were significantly positively related to the presented flux of algal cells in this study ($r=0.66$, $p<0.05$).

In comparison to other subarctic and Arctic seas, the flux rate of chlorophyll *a* in the Bering Sea was of a comparable order of magnitude for early spring (e.g., Michel et al. 1997, Olli et al. 2002, Lalande et al. 2014). While vertical flux patterns vary across the Arctic, there is consistently a large peak during ice melt and break-up, with flux rates rising by several orders of magnitude from early to late spring (e.g. Bauerfeind 1994; Lalande et al. 2009, Lalande et al. 2014). As the highest flux in the Bering Sea was measured on the latest date sampled (May 2, 2009) when ice cover was still 75%, it is likely that the vertical flux rate continued to increase later in the spring as ice melt progressed. The dynamics of vertical flux from sea ice are not yet well understood, as they are controlled by both physical (e.g., temperature, ice ablation, water column stratification; Thomas and Dieckmann 2003) and biological factors (e.g., zooplankton grazing, algal physiology as it affects sinking rate; Smayda 1970; Peinert et al. 2001), and these drivers vary both regionally and seasonally (Peinert et al. 2001).

The proxy used to quantify algae also has an effect on the measured flux rate. Measuring the chlorophyll *a* concentration is often chosen for its simple, efficient and objective technique; however, it is only a rough proxy for the actual quantity of algae. The amount of chlorophyll *a* in a cell varies depending on health, growth status, and adaptations to light conditions (Thomas and Dieckmann 2003), so the carbon to chlorophyll *a* ratio can vary tremendously in different regions and at different times of the year. Calculations of chlorophyll *a* per cell in this study were very high in the sediment trap samples, likely due to the photoacclimation of the algae (Table 2), so using pigment data alone could overestimate algal biomass. Furthermore, chlorophyll *a* concentrations fail to include empty frustules, which can provide information about the overall quality of the food that is exported. Other estimates of biogenic flux rates use particulate organic carbon (e.g., Moran et al. 2005; Fahl and Nöthig 2007), which, although useful, is not exclusive to algae and contains other carbon sources including zooplankton, heterotrophic bacteria, and

detritus. Measurements of biogenic silicate can be used specifically to estimate the contribution of diatoms, radiolarians and silicoflagellates (e.g., Wefer and Fischer 1991; Fahl and Nöthig 2007), but these measurements do not provide information about community composition. It is only by using cell counts that algal cells can be directly enumerated and these numbers compared across space and time. While counting cells is slower, more subjective, and can be biased towards large and well-preserved organisms, it is the only method that allows us to assess the relative contribution of different species, which is essential for comparing the community composition in different domains and addressing species-specific questions about algal fate.

Fate of ice algae

During the period of ice growth, the high vertical flux rate and low phytoplankton standing stock indicated the release of ice algae into the water, which is supported by the strong similarity in the species inventory in ice and traps. However, the relative species composition for ice and water was different during this period and there was no correlation between the two sample sets (Fig. 5A). One explanation for such differences can be episodic release of ice algal cells into the water; the phytoplankton is seeded with ice algae, followed by the selection of ice species that are best adapted to growth in the water column resulting in similar species inventories but different and uncorrelated proportions of each species in the ice and the water. The significantly higher proportion of centric diatoms in the water compared with the ice supports this theory, as centric taxa typically dominant in the summer phytoplankton in the Bering Sea, although they play a minor role among the ice algae. Furthermore, there were significantly lower proportions of *Nitzschia frigida* in the water than in the ice; as a classically ice-associated species, *N. frigida* is rarely found anywhere among the phytoplankton, in agreement with its diminished proportion there observed in this study. The same relative species composition in the water and the traps during the ice growth period suggests that a large portion of the algal cells in the water column—either phytoplankton or released ice algae—sank directly to the benthos, independent of ice-water species differences.

During the period of ice melt, the relative species composition in the ice and the water were the same and were significantly correlated, showing a stronger and more consistent

connection between the ice and the water than during the ice growth period (Fig. 5B). This merging of ice and water domains is characteristic of ice melt in seasonally ice-covered regions, marked by high vertical flux rates and the presence of ice algal species in the water column as the ice ceases to exist as a habitat and its contents are deposited into the water (Leu et al. 2014).

The fate of the ice algal community during ice melt varies across the Arctic: cells can sink to the benthos, be grazed in the water column, or remain viable and contribute to the phytoplankton by seeding the spring bloom (Legendre et al. 1981; Riebesell et al. 1991; Durbin and Casas 2014). Algae will preferentially sink if cells are unhealthy or prone to forming aggregates, increasing their sinking rate; high abundances of zooplankton can deflect a significant flux of cells into the pelagic food web, reducing the amount exported to the benthos. Favorable environmental conditions (i.e., sufficient light and water column stratification) coupled with healthy ice algal cells and low grazing will allow for the growth of ice algae among the phytoplankton. In the Bering Sea, I found no evidence for the formation of aggregates that would increase the export of ice algae beneath the ice. The rapid export of the Arctic sea ice diatom *Melosira arctica*, which can account for up to 85% of the total carbon export under the ice (Boetius et al. 2013), was not detected in this study as *M. arctica* only rarely occurred in the ice in the Bering Sea and was completely absent from the trap samples. The species composition of algae exported beneath the ice in the Bering Sea was significantly different from the species composition in the ice during the period of ice melt, with higher proportions of *Nitzschia frigida* in the ice and higher proportions of species forming ribbon-colonies in the traps, indicating that ice algal fate differs among species. These changes to the algal composition could have been caused by a number of different factors, discussed below.

One possible factor influencing algal composition is grazing pressure. Although zooplankton grazing in the Bering Sea is typically low in the cold water during early spring (Coyle and Cooney 1988), molecular analysis of gut contents show that even during cold years *Calanus glacialis* grazes on ice algae during the early spring, and the pulses of algae released from the ice prior to ice melt "jump start" *C. glacialis'* feeding and reproduction (Durbin and Casas 2014). Therefore, zooplankton grazing could have played a role in altering ice algal fate. The lack of corresponding fecal pellets in the trap samples could be a function of the high assimilation efficiency of Arctic copepods, which can be up to 90% (Conover and Huntley

1991); loss of fecal pellets through coprophagy or coprorhexy could also account for their low numbers (Iversen and Poulsen 2007). It may also have been due to the timing of the trap deployments, which only occurred during daytime hours, and therefore may have missed the flux of fecal pellets from zooplankton grazing during diel vertical migration. Significant grazing has been documented for microzooplankton both before and during the spring phytoplankton bloom in the Bering Sea (Sherr et al. 2013). While these herbivorous protists consume a much larger range of phytoplankton size classes than traditionally believed (Sherr et al. 2013), ice algal and phytoplankton species that form large chains (i.e., *Fragilariopsis* spp.) may still escape this grazing pressure, resulting in preferential grazing of the smaller solitary cells. This could explain the larger proportion of chain-forming species in the traps relative to the ice.

Differential sinking rates could also alter the relative species composition between the ice and the traps. The sinking rate of a cell depends on its size, shape and physiology as well as its tendency for aggregation. On average, the sinking rate of a solitary diatom is ~0.50 m day^{-1} (Eppley et al. 1967); however, chains of cells can sink much faster: in some cases, a 10-cell increase in colony length can as much as quadruple the sinking rate (Smayda 1971). Long colonies of *Fragilariopsis* spp. and *Fossula arctica*, which were often over 50 cells in length, likely sank at a rapid rate, resulting in their high proportions in the sediment traps. It is important to note that not only did different sinking rates influence the rate at which different species were collected in the traps, but they also dictated how large the temporal disconnect was between the ice and the trap samples. For example, small solitary cells may have taken up to two weeks to reach the traps at 5 m depth, during which time the community in the ice may have shifted, while large colonies could have been representatives of the ice algal community only days before.

Although lateral advection and resuspension from sediment could have caused differences in the relative species composition between ice and traps, similar differences in algal composition in the ice and traps as found in this study have been observed elsewhere. In Baffin Bay, Michel et al. (2002) saw the same pattern in the relative species composition with higher proportions of *N. frigida* in the ice and higher proportions of *Fragilariopsis* spp. in the traps, suggesting that the differences may be specific to taxa rather than location. *N. frigida* may dissociate from its characteristic branching colonies when it senesces in the water column, and thus be counted among the unknown pennate diatoms, resulting in underestimates in sediment

trap samples. *Fragilariopsis* spp. have a very low specific dissolution rate due to the structure and composition of its frustule (Passow et al. 2011), which could result in its accumulation in the traps. In Antarctic waters, comparisons of species between ice and sediment traps suggest that lightly silicified frustules are rapidly recycled in the water column (Leventer and Dunbar 1987); however, there is no evidence for silicate dissolution in the subarctic Pacific even over much greater depths (Takahashi 1986), and it is unlikely to have been an issue in this study doe to the shallow depth of the traps.

Although I did not capture the start of the spring phytoplankton bloom during the sampling years, and my data show the propensity for algal cells to sink in large quantities during the spring, ice algal fate likely changes as ice melt progresses. Virtually all ice algal species in the Bering Sea are capable of growing in the water column, and although it is difficult to assess viability in fixed cells, the majority of cells in the water showed no degradation in their chloroplast structure and the cells appeared to be healthy. These cells may have been highly low-light adapted; using cell counts from this study and chlorophyll *a* concentrations from the same stations, I estimated that the average chlorophyll content in the sub-ice phytoplankton was 24 pg cell^{-1}, higher than for typical phytoplankton cells (1-12 pg chl *a* cell^{-1}; Sosik et al. 1989) and over three times higher than the estimate of chlorophyll *a* content of cells in the overlying ice (on average 7 pg cell^{-1}). While it is possible that this is an overestimation due to the exclusion of small cells in my counts, chlorophyll *a* contents of this magnitude have been found in highly photoacclimated ice algal cells under similar light conditions (Gosselin et al. 1990). Although phytoplankton growth rates under the ice in the Bering Sea were low (< 0.1 d^{-1}), they increased significantly as soon as bloom conditions developed (Sherr et al. 2013). This suggests that although extensive ice cover held off the development of the phytoplankton bloom at least into early May, when the ice ultimately retreated, the water was primed for the spring ice-edge bloom with viable ice algal species.

Additional evidence supports ice algal seeding in the Bering Sea. Model forecasts of primary production in the southeastern Bering Sea are more predictive when ice algal seeding is incorporated in the ice-edge bloom (Jin et al. 2007). The timing of the spring bloom matches that of the receding ice in the Bering Sea (Alexander and Chapman 1981), unlike some regions where there is a large temporal disconnect (Horner and Schrader 1982, and references therein). The

results of this study in addition to those findings suggest that ice algae do seed the spring phytoplankton bloom in the Bering Sea, as is common in many other subarctic and Arctic seas (e.g., Legendre et al. 1981; Michel et al. 1993; Haecky et al. 1998).

According to the Oscillating Control Hypothesis (Hunt and Stabeno 2002), ice algae could only seed the spring ice-edge bloom if the timing of ice melt is late enough that it coincides with sufficient irradiance for phytoplankton growth. In 2008 and 2009, this was extremely likely, as the ice was still in the early stages of melt in early May when the day length exceeded 16.50 hrs. However, if the ice melts early in the spring, as occurs during warm years, there is insufficient light for phytoplankton growth and the ice-edge bloom does not occur; instead, a later open-water bloom develops when solar heating rather than melt water stratifies the water column (Hunt and Stabeno 2002). Although there is no significant difference in the magnitude of spring blooms during warm versus cold years (Sigler et al. 2014), the timing of the bloom has tremendous implications for the fate of primary production. During cold years, as sampled in this study, there is a mismatch between the timing of the ice edge-bloom and the phenology of zooplankton development, so the bloom is primarily exported to the benthos, while in warm years the late development of the bloom coincides with that of zooplankton populations, which readily graze the available algae, diverting energy into the pelagic system (Sigler et al. 2014). Therefore, the seasonal ice extent has tremendous implications for the overall ecosystem of the Bering Sea.

Unlike most Arctic seas, where sea ice is declining rapidly, there has so far been no decrease in annual sea ice extent in the Bering Sea (Brown and Arrigo 2012). However, much of ice growth in the Bering Sea is driven by cold northerly Arctic air creating a "conveyor belt" of ice production in northern polynas and then advecting it south across the shelf (Pease 1980). As Arctic air temperatures are rising at twice the global rate (Pachauri and Reisinger 2007), northerly winds will continue to warm, which may ultimately have a large effect on the development of Bering Sea ice. This could result in a higher proportion of warm years in the Bering Sea with reduced ice extent and earlier ice retreat. Under these conditions, a larger portion of the ice algal production would be exported to the benthos during ice melt, but the ice algal contribution to seeding the phytoplankton would become negligible, and when the open-water bloom developed later in the summer, high zooplankton grazing would keep more of this

production in the pelagic realm. Thus, the majority of the material exported to the benthos would more likely be in the form of fecal pellets rather than ungrazed algal cells.

Presumably, sufficient warming could result in the permanent loss of sea ice off the southern shelf, eliminating all input from ice algae, which could have noticeable effects on benthic communities. But even drastic climate change would be unlikely to have such an effect. Climate models show that a doubling atmospheric CO_2 and increased temperatures by as much as 2°C would result only in an increase in warm-year conditions but nowhere near complete ice loss in the Bering Sea (Lee et al. 2012). Ice extent would be reduced by 300-400 km in southern latitudes of the Bering Sea but the mid-latitude shelf would remain ice covered through March, much like during warm years today. The Bering Sea's seasonal ice cover is likely to remain one of its most defining characteristics even in the face of a warming climate.

Conclusions

I present here the results of the first quantitative assessment of Bering Sea ice algal communities, which have a community composition similar to many of those in other Arctic regions. Ice algal abundance was high in the Bering Sea throughout the spring, and continued to increase during the late spring period of ice melt. The growth of ice algae during the spring is essential for grazers as phytoplankton abundance beneath the ice remained very low during these cold years, with no increase in magnitude even as late as May 1st. The phytoplankton present during the spring were seeded from the ice; phytoplankton communities appeared to be influenced first by the episodic input from the ice algal community during the period of ice growth and then by the more regular release of cells from the ice during the period of ice melt. Due to the cold conditions in the Bering Sea during this study, I did not observe the development of the spring phytoplankton bloom from March-May; however, these results show that the existing phytoplankton community prior to the ice retreat was comprised of healthy ice algal cells that would be in place to seed the ice-edge bloom.

I further found that there was a substantial vertical flux of algal cells beneath the ice, which began as early as mid-March, suggesting that the export of sympagic primary production

to the benthos may be greater than previously predicted and is not restricted to the period of ice melt. Due to the relatively low zooplankton grazing pressures in the cold water, the vast majority of primary production is exported in the form of "fresh" algal cells rather than fecal pellets, and it is, therefore, a rich source of food for benthic organisms long before the ice melts.

My study characterizes the dynamics of ice algal and phytoplankton communities during two cold springs in the Bering Sea. Although it is restricted to only a two month period, it can be used as a baseline for interactions between ice algae and phytoplankton and the underlying benthos under ice-covered spring conditions. These interactions will differ substantially as conditions change during warm years in the Bering Sea, which may become more prevalent in the future, increasing our need to understand the connection between sympagic, pelagic and benthic communities in the Bering Sea.

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Appendix

Table A-1. Station MN4 (169.655ºW, 59.9ºN). Sampled April 4, 2008 during the ice growth period.

Species	Ice algal abundance (cells l^{-1})	Phytoplankton abundance (cells l^{-1})	Flux rate (cells m^{-2} day^{-1})
Biddulphia sp	0	0	138060
Ceratoneis closterium	16800	0	138060
Cocconeis sp. 1	0	120	276120
Coscinodiscus spp.	0	20	0
Entomoneis sp. 1	0	0	69030
Entomoneis sp. 2	16800	0	0
Fossula arctica	13200	0	0
Fragilariopsis spp.	556800	1580	31201591
Gyrosigma sp. 1	9600	80	0
Navicula directa	30000	60	345150
Navicula granii	0	0	69030
Navicula kariana var. *detersa*	88800	0	207090
Navicula septentrionalis	36000	0	2277992
Navicula trigonocephala var. *depressa*	10800	0	0
Navicula valida	27600	0	0
Navicula vanhoeffenii	21600	0	0
Nitzschia pellucida	0	0	483210
Nitzschia frigida	1038000	0	17602668
Nitzschia seriata	0	0	138060
Nitzschia sp. 1	30000	0	621271
Paralia sulcata	0	640	12080262
Pauliella taeniata	0	0	276120
Pinnularia quadratarea var. *constricta*	0	0	207090
Pinnularia sp. 1	19200	0	0
Pleurosigma spp.	6000	0	207090
Pleurosigma tenuiforme	0	0	69030
Pseudogomphonema groenlandicum	21600	0	69030
Pseudogomphonema septentrionale	48000	0	0
Thalassionema nitzschioides	0	40	138060
Thalassiosira spp.	6000	60	207090

Table A-1, continued

Unidentified pennate diatoms	849600	160	15255645
Unidentified centric diatoms	0	80	0
Empty pennate diatoms	0	190	6143676
Empty centric diatoms	0	0	69030
Unidentified flagellates	0	20	69030
Dinoflagellates	0	80	207090
Total cells	2846400	3130	88565579
Total cells (excluding empty)	2846400	2940	82352872

Table A-2. Station MN8.5 (172.766ºW, 59.924ºN). Sampled April 6, 2008 during the ice growth period.

Species	Ice algal abundance (cells l^{-1})	Phytoplankton abundance (cells l^{-1})	Flux rate (cells m^{-2} day^{-1})
Entomoneis sp. 1	500000	0	0
Fragilariopsis spp.	19200000	0	0
Gyrosigma sp. 1	2200000	0	36343
Navicula directa	100000	20	0
Navicula kariana var. *detersa*	100000	0	0
Navicula septentrionalis	1050000	0	0
Navicula vanhoeffenii	500000	0	0
Nitzschia frigida	6100000	80	0
Pauliella taeniata	2150000	0	0
Pinnularia quadratarea var. *constricta*	100000	0	0
Pseudogomphonema groenlandicum	50000	0	0
Pseudogomphonema septentrionale	150000	0	0
Thalassionema nitzschioides	0	120	36343
Unidentified pennate diatoms	7300000	180	290745
Empty pennate diatoms	0	130	0
Total cells	39500000	530	363432
Total cells (excluding empty)	39500000	400	363432

Table A-3. Station DLN2 (173.695ºW, 63.266ºN). Sampled March 19, 2009 during the ice growth period. No water samples available from this station.

Species	Ice algal abundance (cells l^{-1})	Phytoplankton abundance (cells l^{-1})	Flux rate (cells m^{-2} day^{-1})
Ceratoneis closterium	215021	n/a	860093
Chaetoceros spp.	109705		0
Cocconeis sp. 1	0		3440373
Entomoneis sp. 1	245738		860093
Entomoneis sp. 2	0		860093
Fossula arctica	83376		0
Fragilariopsis spp.	2268692		64506988
Navicula directa	13165		0
Navicula granii	228186		0
Nitzschia pellucida	35105		0
Nitzschia frigida	245738		0
Nitzschia seriata	443207		22362423
Nitzschia sigmoidea	105316		1720186
Nitzschia sp. 1	4388		0
Nitzschia sp. 2	92152		2580280
Pauliella taeniata	0		17201864
Pleurosigma spp.	13165		2580280
Pleurosigma tenuiforme	0		860093
Pseudogomphonema septentrionale	4388		0
Thalassiosira spp.	21941		9461025
Unidentified pennate diatoms	535359		6880745
Unidentified centric diatoms	0		5160559
Empty pennate diatoms	160169		12471351
Empty centric diatoms	0		5160559
Unidentified flagellates	4388		0
Total cells	4829198		156967005
Total cells (excluding empty)	4669030		139335095

Table A-4. Station NWC1 (172.316ºW, 63.485ºN). Sampled March 17, 2009 during the ice growth period.

Species	Ice algal abundance (cells l^{-1})	Phytoplankton abundance (cells l^{-1})	Flux rate (cells m^{-2} day^{-1})
Ceratoneis closterium	107829	60	404087
Chaetoceros spp.	0	80	1558621
Entomoneis sp. 1	15543	40	0
Entomoneis sp. 2	5829	0	0
Fossula arctica	34971	0	0
Fragilariopsis spp.	501257	960	2309068
Gyrosigma sp. 1	2914	0	519540
Gyrosigma sp. 3	8743	0	0
Navicula directa	7771	0	0
Navicula kariana var. *detersa*	4857	0	115453
Navicula septentrionalis	153486	0	0
Navicula vanhoeffenii	15543	0	0
Nitzschia pellucida	64114	0	230907
Nitzschia frigida	344857	0	0
Nitzschia seriata	45657	0	0
Nitzschia sp. 1	20400	0	0
Paralia sulcata	0	0	288633
Pauliella taeniata	129200	320	461814
Pinnularia quadratarea var. *constricta*	3886	0	0
Pinnularia sp. 4	13600	0	0
Pleurosigma tenuiforme	0	20	288633
Pseudogomphonema septentrionale	10686	0	0
Thalassiosira spp.	2914	60	0
Unidentified pennate diatoms	450743	160	1096807
Unidentified centric diatoms	7771	180	57727
Empty pennate diatoms	12629	0	4127459
Empty centric diatoms	0	0	981354
Unidentified flagellates	3886	0	0
Total cells	1969086	1880	12440103
Total cells (excluding empty)	1956457	1880	7331290

Table A-5. Station SEC2 (170.958ºW, 62.594ºN). Sampled March 19, 2009 during the ice growth period.

Species	Ice algal abundance (cells l^{-1})	Phytoplankton abundance (cells l^{-1})	Flux rate (cells m^{-2} day^{-1})
Ceratoneis closterium	260204	80	794360
Chaetoceros spp.	0	440	3610725
Cocconeis sp. 1	0	60	144429
Coscinodiscus spp.	0	0	144429
Entomoneis sp. 1	86735	0	144429
Entomoneis sp. 2	86735	0	0
Fossula arctica	0	40	794360
Fragilariopsis spp.	398980	1020	1516505
Gyrosigma sp. 1	17347	0	0
Gyrosigma sp. 3	17347	0	0
Haslea sp. 1	52041	0	0
Navicula algida	34694	0	0
Navicula directa	381633	0	72215
Navicula granii	69388	0	0
Navicula kariana var. *detersa*	329592	0	0
Navicula transitans var. *derasa*	0	20	0
Navicula trigonocephala var. *depressa*	17347	0	0
Navicula valida	34694	0	144429
Nitzschia pellucida	277551	0	144429
Nitzschia frigida	2012245	0	1877577
Nitzschia sigmoidea	156122	0	288858
Nitzschia sp. 1	260204	0	361073
Paralia sulcata	0	0	1949792
Pinnularia quadratarea var. *constricta*	17347	0	0
Pinnularia quadratarea var. *densestriata*	34694	0	0
Pinnularia sp. 4	138776	0	0
Pleurosigma spp.	52041	0	0
Pleurosigma tenuiforme	0	40	361073
Pseudogomphonema groenlandicum	69388	0	0
Pseudogomphonema septentrionale	86735	0	216644
Thalassiosira spp.	0	20	1877577
Unidentified pennate diatoms	2497959	140	3249653
Empty pennate diatoms	0	420	3249653
Empty centric diatoms	0	40	577716

Table A-5, continued

Unidentified flagellates	0	0	144429
Total cells	7389796	2320	21664352
Total cells (excluding empty)	7389796	1860	17836983

Table A-6. Station MK1 (168.951ºW, 62.728ºN). Sampled 3/22/2009 during the ice growth period.

Species	Ice algal abundance (cells l^{-1})	Phytoplankton abundance (cells l^{-1})	Flux rate (cells m^{-2} day^{-1})
Ceratoneis closterium	35943	80	2315775
Chaetoceros spp.	0	280	4824532
Cocconeis sp. 1	0	0	1543850
Cocconeis sp. 2	0	0	192981
Coscinodiscus spp.	0	0	385963
Entomoneis sp. 1	34971	20	0
Entomoneis sp. 2	1943	0	0
Fossula arctica	0	0	771925
Fragilariopsis spp.	167086	1060	3859625
Gyrosigma sp. 1	971	0	385963
Gyrosigma sp. 3	30114	20	0
Navicula directa	48571	80	0
Navicula kariana var. *detersa*	43714	0	0
Navicula septentrionalis	15543	0	0
Navicula valida	11657	20	0
Navicula vanhoeffenii	15543	0	0
Nitzschia pellucida	198171	80	0
Nitzschia frigida	369143	0	0
Nitzschia seriata	12629	0	0
Nitzschia sp. 1	65086	20	0
Paralia sulcata	0	380	2508757
Pinnularia quadratarea var. *bicontracta*	10686	0	0
Pinnularia quadratarea var. *constricta*	3886	0	0
Pinnularia quadratarea var. *cuneata*	9714	0	0

Table A-6, continued

Pinnularia quadratarea var. *dubia*	0	0	192981
Pinnularia sp. 3	14571	0	0
Pinnularia sp. 4	46629	20	0
Pleurosigma spp.	20400	20	0
Pleurosigma tenuiforme	0	20	385963
Pseudogomphonema groenlandicum	4857	0	192981
Pseudogomphonema septentrionale	15543	40	0
Stenoneis inconspicua	26229	0	0
Thalassionema nitzschioides	0	120	771925
Thalassiosira spp.	0	0	3666644
Unidentified pennate diatoms	919943	240	16403408
Unidentified centric diatoms	1943	180	20841977
Empty pennate diatoms	6800	1380	48920752
Unidentified flagellates	2914	0	192981
Dinoflagellates	0	0	192981
Total cells	2135200	4060	108551965
Total cells (excluding empty)	2128400	2680	59631213

Table A-7. Station WAL12 (169.255ºW, 62.112ºN). Sampled 3/23/2009 during the ice growth period.

Species	Ice algal abundance (cells l^{-1})	Phytoplankton abundance (cells l^{-1})	Flux rate (cells m^{-2} day^{-1})
Ceratoneis closterium	59925	840	393120
Chaetoceros spp.	0	160	2162162
Cocconeis sp. 1	0	120	294840
Coscinodiscus spp.	0	40	196560
Entomoneis sp. 1	1677903	1920	98280
Entomoneis sp. 2	119850	0	0
Fossula arctica	29963	160	3783784
Fragilariopsis spp.	4299625	7160	4471744
Gyrosigma sp. 1	59925	80	245700
Gyrosigma sp. 3	134831	160	0

Table A-7, continued

Haslea sp. 1	44944	0	0
Melosira arctica	44944	0	0
Navicula algida	29963	0	0
Navicula directa	179775	280	245700
Navicula kariana var. *detersa*	314607	200	245700
Navicula septentrionalis	1318352	1000	0
Navicula transitans	74906	40	393120
Navicula trigonocephala	44944	0	0
Navicula trigonocephala var. *depressa*	74906	40	0
Navicula valida	0	240	0
Navicula vanhoeffenii	269663	0	0
Nitzschia pellucida	599251	880	1425061
Nitzschia frigida	958801	3120	982801
Nitzschia seriata	434457	0	0
Nitzschia sigmoidea	119850	240	0
Nitzschia sp. 1	179775	80	0
Nitzschia sp. 2	44944	0	147420
Paralia sulcata	0	560	1031941
Pauliella taeniata	0	0	245700
Pinnularia quadratarea var. *bicontracta*	44944	0	0
Pinnularia quadratarea var. *capitata*	14981	0	0
Pinnularia quadratarea var. *constricta*	89888	80	0
Pinnularia quadratarea var. *cuneata*	59925	0	0
Pinnularia quadratarea var. *densestriata*	14981	0	49140
Pinnularia quadratarea var. *dubia*	14981	0	0
Pinnularia quadratarea var. *maxima*	0	80	0
Pinnularia sp. 1	134831	0	0
Pinnularia sp. 4	239700	160	0
Pleurosigma tenuiforme	0	80	687961
Pseudogomphonema groenlandicum	494382	120	0
Pseudogomphonema septentrionale	314607	40	0
Stenoneis inconspicua	149813	0	0
Thalassionema nitzschioides	0	80	196560
Thalassiosira spp.	0	120	196560
Unidentified pennate diatoms	7790262	6560	1179361
Unidentified centric diatoms	0	360	0
Empty pennate diatoms	0	2120	3366093
Empty centric diatoms	0	140	294840
Dinoflagellates	0	0	49140

Table A-7, continued

Total cells	20479401	27260	22383292
Total cells (excluding empty)	20479401	25000	18722359

Table A-8. Station MK1B (169.023ºW, 62.699ºN). Sampled March 25, 2009 during the ice growth period.

Species	Ice algal abundance (cells l^{-1})	Phytoplankton abundance (cells l^{-1})	Flux rate (cells m^{-2} day^{-1})
Ceratoneis closterium	14907	180	1038096
Chaetoceros spp.	2080	120	655640
Cocconeis sp. 2	0	0	54637
Coscinodiscus spp.	347	0	109273
Entomoneis sp. 1	2773	0	218547
Fossula arctica	0	580	109273
Fragilariopsis spp.	119253	1100	5299753
Gyrosigma sp. 1	0	0	109273
Gyrosigma sp. 3	0	20	163910
Navicula directa	6240	0	218547
Navicula kariana var. *detersa*	5200	60	163910
Navicula septentrionalis	10400	0	0
Navicula superba	6587	0	0
Nitzschia pellucida	69333	100	764913
Nitzschia frigida	89440	60	3988474
Nitzschia sigmoidea	5893	0	0
Nitzschia sp. 1	23573	0	0
Nitzschia sp. 2	3120	0	0
Paralia sulcata	1040	80	273183
Pauliella taeniata	0	100	0
Pinnularia quadratarea var. *bicontracta*	347	0	0
Pinnularia quadratarea var. *constricta*	1040	0	0
Pinnularia quadratarea var. *dubia*	1040	0	0
Pinnularia sp. 4	4160	20	218547
Pleurosigma spp.	1387	0	0
Pleurosigma tenuiforme	347	0	273183

Table A-8, continued

Pseudogomphonema groenlandicum	1040	0	0
Pseudogomphonema septentrionale	14213	40	273183
Thalassiosira spp.	5547	40	109273
Unidentified pennate diatoms	172293	440	1529826
Unidentified centric diatoms	693	0	0
Empty pennate diatoms	29120	1890	4862660
Empty centric diatoms	0	60	355138
Unidentified flagellates	693	0	0
Dinoflagellates	693	0	0
Total cells	592800	4890	20789236
Total cells (excluding empty)	563680	2940	15571438

Table A-9. Station NWC3 (173.387ºW, 62.682ºN). Sampled March 27, 2009 during the ice growth period.

Species	Ice algal abundance (cells l^{-1})	Phytoplankton abundance (cells l^{-1})	Flux rate (cells m^{-2} day^{-1})
Ceratoneis closterium	2702	260	726952
Chaetoceros spp.	676	300	1696222
Cocconeis sp. 3	0	20	0
Coscinodiscus spp.	169	0	848111
Entomoneis sp. 1	0	20	0
Fossula arctica	0	640	0
Fragilariopsis spp.	0	3420	8602270
Gyrosigma sp. 1	169	40	0
Navicula directa	591	180	0
Navicula septentrionalis	0	0	3392445
Paralia sulcata	0	180	1938540
Pauliella taeniata	0	0	2302016
Pinnularia quadratarea var. *constricta*	169	0	0
Pleurosigma tenuiforme	0	20	121159
Thalassiosira spp.	2364	100	2907810
Unidentified pennate diatoms	9711	2500	9935016

Table A-9, continued

Unidentified centric diatoms	2027	340	4725191
Empty pennate diatoms	0	520	17143961
Empty centric diatoms	0	60	0
Total cells	56450	7680	32470540
Total cells (excluding empty)	44375	5080	19627715

Table A-10. Station MN4.5 (169.938ºW, 59.937ºN). Sampled April 7, 2009 during the ice growth period. No water samples available from this station.

Species	Ice algal abundance (cells l^{-1})	Phytoplankton abundance (cells l^{-1})	Flux rate (cells m^{-2} day^{-1})
Actinoptychus spp.	0	n/a	580737
Ceratoneis closterium	122222		0
Chaetoceros spp.	244444		3194054
Cocconeis sp. 1	0		725921
Coscinodiscus spp.	0		1016290
Entomoneis sp. 1	4400000		0
Entomoneis sp. 2	366667		0
Fossula arctica	122222		0
Fragilariopsis spp.	45038889		13792508
Navicula directa	61111		0
Navicula kariana var. *detersa*	122222		0
Navicula septentrionalis	1283333		0
Navicula transitans	61111		145184
Navicula trigonocephala var. *depressa*	61111		0
Navicula valida	183333		0
Navicula vanhoeffenii	611111		0
Nitzschia pellucida	2200000		0
Nitzschia delicatissima	611111		0
Nitzschia frigida	7088889		0
Nitzschia seriata	1222222		0
Nitzschia sigmoidea	0		725921
Nitzschia sp. 1	61111		0
Nitzschia sp. 2	366667		290369

Table A-10, continued

Odontella aurita	61111	435553
Paralia sulcata	0	14663614
Pleurosigma spp.	61111	290369
Pseudogomphonema groenlandicum	122222	0
Pseudogomphonema septentrionale	916667	0
Thalassionema nitzschioides	0	725921
Unidentified pennate diatoms	10877778	1451843
Empty pennate diatoms	0	580737
Empty centric diatoms	0	1234067
Dinoflagellates	0	290369
Total cells	76266667	40143458
Total cells (excluding empty)	76266667	38328654

Table A-11. Station MN15 (176.416ºW, 59.902ºN). Sampled April 10, 2008 during the ice melt period.

Species	Ice algal abundance (cells l^{-1})	Phytoplankton abundance (cells l^{-1})	Flux rate (cells m^{-2} day^{-1})
Entomoneis sp. 1	0	200	187824
Fragilariopsis spp.	4344569	8500	187260715
Gyrosigma sp. 1	284644	200	610429
Navicula directa	14981	0	0
Navicula kariana var. *detersa*	209738	0	0
Navicula septentrionalis	14981	1200	2629539
Navicula valida	14981	0	0
Nitzschia frigida	2112360	1600	3521704
Nitzschia seriata	0	0	375648
Pauliella taeniata	14981	0	3568660
Pinnularia quadratarea var. *constricta*	0	100	0
Pinnularia quadratarea var. *dubia*	89888	0	0
Pseudogomphonema groenlandicum	119850	0	0
Pseudogomphonema septentrionale	434457	0	0
Thalassionema nitzschioides	0	0	281736

Table A-11, continued

Thalassiosira spp.	149813	0	1126945
Unidentified pennate diatoms	3775281	7800	22163254
Empty pennate diatoms	0	0	4695605
Unidentified flagellates	74906	0	0
Dinoflagellates	14981	0	0
Total cells	11670412	19600	226422058
Total cells (excluding empty)	11670412	19600	221726454

Table A-12. Station SL8.25 (172.830ºW, 62.074ºN). Sampled April 12, 2008 during the ice melt period.

Species	Ice algal abundance (cells l^{-1})	Phytoplankton abundance (cells l^{-1})	Flux rate (cells m^{-2} day^{-1})
Ceratoneis closterium	36620	0	325866
Coscinodiscus spp.	0	0	65173
Entomoneis sp. 1	1757746	140	260693
Fossula arctica	21898592	36820	4431777
Fragilariopsis spp.	81112676	13780	72146726
Gyrosigma sp. 1	402817	40	65173
Navicula directa	36620	60	0
Navicula septentrionalis	1904225	0	2378822
Nitzschia frigida	2490141	520	293279
Nitzschia seriata	0	520	0
Nitzschia sp. 2	0	0	619145
Paralia sulcata	0	0	391039
Pauliella taeniata	1464789	3740	1042771
Pleurosigma tenuiforme	0	0	195520
Pseudogomphonema septentrionale	36620	0	0
Thalassiosira spp.	0	1800	2215889
Unidentified pennate diatoms	14940845	7760	11144616
Unidentified centric diatoms	0	40	293279
Empty pennate diatoms	0	170	1156824
Empty centric diatoms	0	0	146640

Table A-12, continued

Unidentified flagellates	0	0	97760
Dinoflagellates	0	0	65173
Total cells	126081690	65390	97336166
Total cells (excluding empty)	126081690	65220	96032702

Table A-13. Station W7.5 (171.267ºW, 59.894ºN). Sampled April 16, 2008 during the ice melt period.

Species	Ice algal abundance (cells l^{-1})	Phytoplankton abundance (cells l^{-1})	Flux rate (cells m^{-2} day^{-1})
Ceratoneis closterium	328386	100	0
Entomoneis sp. 1	328386	0	0
Entomoneis sp. 2	32839	0	0
Fossula arctica	0	540	0
Fragilariopsis spp.	18126902	18400	4736609
Gyrosigma sp. 1	558256	60	87715
Navicula directa	459740	40	263145
Navicula granii	525417	0	0
Navicula kariana var. *detersa*	1346382	0	175430
Navicula septentrionalis	492579	0	0
Navicula valida	164193	0	0
Nitzschia frigida	2265863	60	0
Nitzschia seriata	229870	0	0
Nitzschia sp. 2	0	140	0
Odontella aurita	0	0	87715
Paralia sulcata	0	0	3859459
Pinnularia quadratarea var. *constricta*	361224	0	0
Pleurosigma tenuiforme	65677	0	0
Pseudogomphonema septentrionale	229870	40	0
Thalassionema nitzschioides	0	140	350860
Thalassiosira spp.	0	1200	526290
Unidentified pennate diatoms	10606865	5400	614005
Unidentified centric diatoms	5319852	0	0
Empty pennate diatoms	0	90	1008722

Table A-13, continued

Unidentified flagellates	65677	0	87715
Total cells	41507978	26210	11797666
Total cells (excluding empty)	41507978	26120	10788943

Table A-14. Station ST110 (172.555ºW, 62.260ºN). Sampled April 28, 2008 during the ice melt period.

Species	Ice algal abundance (cells l^{-1})	Phytoplankton abundance (cells l^{-1})	Flux rate (cells m^{-2} day^{-1})
Ceratoneis closterium	32484	0	0
Fossula arctica	0	0	262342752
Fragilariopsis spp.	7406369	2320	37823096
Gyrosigma sp. 1	32484	0	659705
Navicula directa	97452	80	219902
Navicula granii	129936	0	0
Navicula kariana var. *detersa*	32484	0	439803
Navicula pelagica	259873	0	0
Nitzschia frigida	11174522	0	9675676
Nitzschia seriata	0	0	439803
Paralia sulcata	0	720	659705
Pauliella taeniata	5814650	0	1979115
Pseudogomphonema septentrionale	32484	0	0
Thalassiosira spp.	584713	120	1759214
Unidentified pennate diatoms	5424841	1000	6597052
Unidentified centric diatoms	0	0	659705
Empty pennate diatoms	0	0	549754
Dinoflagellates	0	40	0
Total cells	31022293	4280	323255528
Total cells (excluding empty)	31022293	4280	323255528

Table A-15. Station 70M53 (173.630ºW, 61.505ºN). Sampled April 30, 2008 during the ice melt period.

Species	Ice algal abundance (cells l^{-1})	Phytoplankton abundance (cells l^{-1})	Flux rate (cells m^{-2} day^{-1})
Ceratoneis closterium	594824	0	529238
Chaetoceros spp.	0	40	0
Entomoneis sp. 1	0	80	0
Fossula arctica	0	1360	0
Fragilariopsis spp.	62946	1840	8644226
Gyrosigma sp. 1	5948240	160	2028747
Navicula directa	314907	160	529238
Navicula granii	174948	0	0
Navicula kariana var. *detersa*	0	40	0
Nitzschia frigida	10532	120	0
Nitzschia seriata	0	0	352826
Paralia sulcata	0	0	3263636
Pauliella taeniata	40413	0	1058477
Pleurosigma tenuiforme	0	0	352826
Thalassionema nitzschioides	0	0	441032
Thalassiosira spp.	79601	880	2910811
Unidentified pennate diatoms	7522774	2360	3704668
Unidentified centric diatoms	0	120	0
Empty pennate diatoms	0	240	1896437
Unidentified flagellates	34990	80	0
Dinoflagellates	34990	0	0
Total cells	14819166	7480	25712162
Total cells (excluding empty)	14819166	7240	23815725

Table A-16. Station ST28 (176.986ºW, 61.696ºN). Sampled April 14, 2009 during the ice melt period. No water samples available from this station.

Species	Ice algal abundance (cells l^{-1})	Phytoplankton abundance (cells l^{-1})	Flux rate (cells m^{-2} day^{-1})
Ceratoneis closterium	90293	n/a	0
Entomoneis sp. 1	1986436		520906
Fragilariopsis spp.	57245479		10287888
Gyrosigma sp. 1	1986436		130226
Haslea sp. 1	90293		0
Navicula algida	90293		0
Navicula directa	1805851		0
Navicula kariana var. *detersa*	632048		0
Navicula septentrionalis	29615957		1041811
Navicula vanhoeffenii	722340		0
Nitzschia frigida	18690559		5469510
Nitzschia seriata	1354388		1041811
Nitzschia sigmoidea	2889362		260453
Nitzschia sp. 1	1354388		0
Nitzschia sp. 2	722340		390679
Pauliella taeniata	2076729		0
Pinnularia quadratarea var. *constricta*	361170		260453
Pseudogomphonema groenlandicum	722340		0
Pseudogomphonema septentrionale	902926		0
Unidentified pennate diatoms	15078856		1823170
Unidentified centric diatoms	270878		260453
Empty pennate diatoms	0		586019
Empty centric diatoms	0		130226
Silicoflagellate	130226		0
Total cells	138819588		22203606
Total cells (excluding empty)	138819588		21487361

Table A-17. Station SL1 (167.754ºW, 61.701ºN). Sampled April 18, 2009 during the ice melt period. No water samples available from this station.

Species	Ice algal abundance (cells l^{-1})	Phytoplankton abundance (cells l^{-1})	Flux rate (cells m^{-2} day^{-1})
Ceratoneis closterium	114299	n/a	301763
Chaetoceros spp.	45720		603527
Entomoneis sp. 1	365758		1810580
Fragilariopsis spp.	2468866		62464998
Haslea sp. 1	45720		0
Navicula algida	22860		0
Navicula septentrionalis	160019		0
Navicula trigonocephala var. *depressa*	22860		0
Navicula vanhoeffenii	137159		1207053
Nitzschia pellucida	137159		301763
Nitzschia frigida	5212050		3621159
Nitzschia seriata	160019		0
Nitzschia sigmoidea	45720		301763
Nitzschia sp. 1	297178		301763
Paralia sulcata	0		2414106
Pinnularia quadratarea var. bicontracta	22860		0
Pinnularia quadratarea var. constricta	45720		0
Pinnularia quadratarea var. maxima	22860		0
Pinnularia sp. 4	251459		0
Pleurosigma spp.	274318		1810580
Pseudogomphonema groenlandicum	45720		0
Pseudogomphonema septentrionale	160019		301763
Thalassiosira spp.	0		603527
Unidentified pennate diatoms	2628885		6940555
Unidentified centric diatoms	0		1207053
Empty pennate diatoms	0		1508816
Unidentified flagellates	22860		0
Silicoflagellate	0		301763
Total cells	12710087		86002534
Total cells (excluding empty)	12710087		84493718

Table A-18. Station NP1 (167.798ºW, 59.448ºN). Sampled April 20, 2009 during the ice growth period. No water samples available from this station.

Species	Ice algal abundance (cells l^{-1})	Phytoplankton abundance (cells l^{-1})	Flux rate (cells m^{-2} day^{-1})
Actinoptychus spp.	0	n/a	279974
Biddulphia spp.	0		279974
Ceratoneis closterium	59479		0
Cocconeis sp. 1	0		466623
Cocconeis sp. 2	0		279974
Coscinodiscus spp.	0		746596
Entomoneis sp. 1	1685236		93325
Entomoneis sp. 2	99132		93325
Fossula arctica	257742		1399868
Fragilariopsis spp.	14631813		9985727
Navicula directa	158610		0
Navicula kariana var. *detersa*	297395		0
Navicula transitans	118958		0
Navicula valida	79305		0
Navicula vanhoeffenii	79305		0
Nitzschia pellucida	674094		279974
Nitzschia frigida	3370472		0
Nitzschia sigmoidea	39653		93325
Nitzschia sp. 2	337047		0
Paralia sulcata	674094		10452350
Pinnularia quadratarea var. *constricta*	19826		0
Pinnularia sp. 4	59479		0
Pleurosigma spp.	19826		746596
Pleurosigma teuniforme	0		186649
Pseudogomphonema groenlandicum	39653		0
Pseudogomphonema septentrionale	515484		0
Thalassionema nitzschioides	0		186649
Thalassiosira spp.	0		746596
Unidentified pennate diatoms	3390298		4012956
Unidentified centric diatoms	0		653272
Empty pennate diatoms	89218		233311
Empty centric diatoms	0		839921

Table A-18, continued

Silicoflagellate	0	93325
Total cells	26696120	32150307
Total cells (excluding empty)	26606901	31077075

Table A-19. Station ST92 (173.692ºW, 61.551ºN). Sampled May 1, 2009 during the ice growth period. No water samples available from this station.

Species	Ice algal abundance (cells l^{-1})	Phytoplankton abundance (cells l^{-1})	Flux rate (cells m^{-2} day^{-1})
Ceratoneis closterium	125467	n/a	0
Chaetoceros spp.	0		474093
Entomoneis sp. 1	1317405		632123
Entomoneis sp. 2	62734		0
Fossula arctica	1129204		4345849
Fragilariopsis spp.	6210623		7269420
Gyrosigma sp. 1	313668		0
Gyrosigma sp. 3	0		237046
Haslea sp. 1	62734		0
Navicula directa	376401		79015
Navicula kariana var. *detersa*	188201		0
Navicula septentrionalis	2446609		0
Navicula vanhoeffenii	250934		158031
Nitzschia pellucida	752803		316062
Nitzschia frigida	43348893		0
Nitzschia sigmoidea	878270		0
Nitzschia sp. 1	250934		0
Nitzschia sp. 2	125467		395077
Pinnularia quadratarea var. *constricta*	62734		0
Pinnularia sp. 4	125467		0
Pseudogomphonema septentrionale	815536		0
Thalassiosira spp.	0		1422278
Unidentified pennate diatoms	5520554		711139
Unidentified centric diatoms	0		79015

Table A-19, continued

Empty pennate diatoms	62734	158031
Empty centric diatoms	0	513600
Total cells	64427370	16790779
Total cells (excluding empty)	64364637	16119148

Table A-20. Station BN1 (172.517ºW, 62.251ºN). Sampled May 2, 2009 during the ice growth period. No water samples available from this station.

Species	Ice algal abundance (cells l^{-1})	Phytoplankton abundance (cells l^{-1})	Flux rate (cells m^{-2} day^{-1})
Entomoneis sp. 1	232222	n/a	0
Fossula arctica	24035000		121149017
Fragilariopsis spp.	17823056		185499991
Navicula granii	348333		0
Navicula septentrionalis	9056667		0
Nitzschia frigida	4238056		0
Nitzschia sigmoidea	58056		0
Nitzschia sp. 1	58056		0
Nitzschia sp. 2	116111		0
Pauliella taeniata	41858056		25377849
Pleurosigma tenuiforme	0		604234
Thalassionema nitzschioides	116111		0
Thalassiosira spp.	464444		8761400
Unidentified pennate diatoms	9230833		12991042
Empty pennate diatoms	87083		0
Unidentified flagellates	58056		0
Dinoflagellates	9230833		12991042
Silicoflagellate	87083		0
Total cells	117098056		367374574
Total cells without empty	117010972		367374574